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INSTITUUT VOOR PLANTENZIEKTENKUNDIG ONDERZOEK
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MEDEDELING No. 256

LABORATORIUM VOOR FYTOPATHOLOGIE
WAGENINGEN, NEDERLAND
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MEDEDELING No. 193

YELLOW RUST ON WHEAT
STUDIES IN EPIDEMIOLOGY AND PHYSIOLOGIC SPECIALIZATION

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PESTIBUS OBSTAT INVESTIGATIO

OVERDRUK UIT:
T. PL.-ZIEKTEN, 67: 69-256, 1961

T. Pl.ziekten 67 (1961): 69–256

YELLOW RUST ON WHEAT
STUDIES IN EPIDEMIOLOGY AND PHYSIOLOGIC SPECIALIZATION[1])

Met een samenvatting:

Gele roest op tarwe

Onderzoekingen over zijn epidemiologie en fysiologische specialisatie

BY

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AIS	=	average infection spectrum (24.25)
ARDAP	=	average relative degree of attack percentage (24.25)
c.	=	circa
cal.	=	calory
CI	=	compatibility index (24.41)
cm.	=	centimeter = 0.394 inch
cm^2	=	square centimeter = 0.155 square inch
DA	=	degree of attack (13.6)
GS	=	growth stage (12.11)
ha.	=	hectare = 2.471 acres
IL	=	infection level (24.22)
IT	=	infection type (13.4, 13.5)
LM	=	leaf mass (41)
LMI	=	leaf mass index (41)
m.	=	meter = 1.094 yards
m^2	=	square meter = 1.196 square yards
ml.	=	milliliter
mm.	=	millimeter = 0.039 inch
PC	=	population characteristic (24.41)
RC	=	race characteristic (24.41)
RDA	=	relative degree of attack (24.23)
RDAP	=	relative degree of attack percentage (24.24)
RH	=	relative humidity
RIS	=	relative infection spectrum (24.25)
RPA	=	relative percentage of attack (24.26)
RM	=	rust mass (41)
RMI	=	rust mass index (41)
sq.m.	=	square meter = 1.196 square yards
ø	=	diameter
°C.	=	centigrade

Figures between brackets refer to paragraphs, e.g.: (12.24)

The tables, illustrations and maps bear the numbers of the paragraphs to which they belong, e.g. table 12.11; a table number preceded by A refers to the appendix, e.g. table A.24.42.

– and you've no idea how confusing it is
all the things being alive;

L. Carroll, Alice's Adventures in Wonderland

0 PREFACE

01 INTRODUCTION

In 1955 a severe yellow rust epidemic struck the Netherlands wheat culture. The losses have been estimated at 5,000,000 guilders (BROEKHUIZEN, 1955), c. 10% of the national wheat production. The epidemic caused great disquiet among the wheat growers and breeders. The Netherlands Grain-Centre set up a Committee for Yellow Rust Research, presided over by Professor Dr. A. J. P. OORT. This committee advised the appointment of a scientist to study the epidemiology of yellow rust.

In the autumn of 1955 the writer was invited to undertake this yellow rust investigation under the auspices of the Committee for Yellow Rust Research. The formulation of the subject of research was wide: the Biology and Epidemiology of Yellow Rust on Wheat. For race identification work a close co-operation with the *Biologische Bundesanstalt für Land- und Forstwirtschaft* (Federal Institute of Biology for Agriculture and Forestry, German Federal Republic) at Braunschweig, Germany, was to be established. The international aspects of yellow rust epidemiology were also to receive particular attention. To this purpose an International Yellow Rust Trials Project was started in the autumn of 1955. Funds for assistance, travelling and equipment were provided.

02 THE INTERNATIONAL YELLOW RUST CONFERENCES

On the joint initiative of the *Biologische Bundesanstalt für Land- und Forstwirtschaft* and the Netherlands Grain-Centre, a First European Yellow Rust Conference was held at Braunschweig, Germany, from 20th to 22nd February, 1956. Twenty five scientists from seven European countries attended this conference, where the basis for future international co-operation was laid.

On 23rd and 24th June, 1960, a Second European Yellow Rust Conference was held at Wageningen on the joint invitation of the Netherlands Grain-Centre and the *Biologische Bundesanstalt*. Thirty scientists from eight European countries met to discuss their work, to exchange results and to prepare future co-operation.

03 GERMAN-DUTCH CO-OPERATION

In the summer of 1956 the Netherlands Grain-Centre granted 22,000 DM to the *Biologische Bundesanstalt* to build another greenhouse for the race identification of yellow rust. The *Biologische Bundesanstalt* undertook the task of identifying the yellow rust samples received as a result of the fresh initiative. The new greenhouse came into use in the spring of 1958. The identification work was carried out by Dr. EVA FUCHS, at the *Institut für Physiologische Botanik* of the *Biologische Bundesanstalt*, Braunschweig. The writer kept in close and continual contact with the Braunschweig station.

04 ORGANIZATION

The Netherlands Grain-Centre is a private foundation which serves as a

"subject-association" where representatives of government, farmers, breeders, milling industry, cereals trade and various organizations meet and discuss common problems. One of the tasks of the Netherlands Grain-Centre is the stimulation and eventual finance of research on the production and processing of cereals (malting barley excepted). The Netherlands Grain-Centre itself does not carry out any research but invites a specialized institute to execute a project. In the present case the Institute for Phytopathological Research (I.P.O.) at Wageningen was invited. The writer was appointed as a research officer to the I.P.O., but was seconded to the Laboratory of Phytopathology of the Agricultural University, Wageningen. This unusual procedure was followed since the director of the Laboratory of Phytopathology, Professor OORT, himself thoroughly familiar with yellow rust problems, was the president of the Committee on Yellow Rust Research.

05 FINANCE

The Netherlands Grain-Centre planned a Ten Years' Project on Cereal Research for the finance of research. In this project, which started in 1954, the yellow rust work was incorporated. The funds for the project were obtained from the Board for Grains, Seeds and Pulses and from the Ministry of Agriculture and Fisheries.

This publication covers a period of five years, 1956 to 1960. It is intended as a final report on the investigations into the epidemiology and physiologic specialization of yellow rust, executed at the expense of the Netherlands Grain-Centre.

The publication of this report was made possible by money grants from the Netherlands Grain-Centre, the *Nederlandse Plantenziektenkundige Vereniging* and the Institute for Phytopathological Research (I.P.O.), all in Wageningen.

The writer presents this report to the University of Amsterdam for consideration as a thesis for a doctorate.

1 INTRODUCTION

To set the stage of the research here reported, this introductory chapter discusses some unrelated subjects in a general way; more detailed information will be given in later chapters. Many of the following pages deal with techniques, which, apart from the modifications necessary to meet the special character of yellow rust, are the usual techniques in rust work. The discussion on wheat culture is an original contribution based on the writer's personal investigation.

11 GEOGRAPHICAL SITUATION OF THE NETHERLANDS

11.1 Geographical situation

The Netherlands are a small country on the north-west border of the European continent, situated between 50° 45′ and 53° 3′ NL. In the east the Netherlands are bordered by Germany, in the south by Belgium and in the west and north by the North Sea. The country is a part of the North-west European plain, which stretches from the Pyrenees north along the Atlantic Ocean, bends

eastward along the North and Baltic Sea and tapers out into the great Russian plains.

In this publication the term "North-west Europe" designates that part of Europe, which is situated north of the Pyrenees and the Alps and west of the Baltic Sea and the Polish-German border.

11.2 Climate

The Netherlands climate, as that of most of North-west Europe, belongs to the temperate-humid type of KÖPPEN. The influence of the Gulfstream has a moderating effect on the climate, an effect which diminishes rapidly with increasing distance from the sea. The Dutch climate is an atlantic climate, dominated by depressions passing the Netherlands on their way from the Atlantic to the east or north. The depressions are accompanied by south-westerly winds and rain. High pressure areas over Scandinavia and northern Russia bring dry and cold easterly winds, a weather type predominant in late winter and early spring.

11.3 North-west European wheat area

The North-west European plain forms a belt in which wheat is grown with varying intensity (map 11.3.a, b and c). Large regions with high intensity occur in France, the most important lying near the Franco-Belgian frontier. Small regions with a high wheat intensity can be found in the Netherlands. In south-eastward direction the coastal plains are broken up into smaller entities by mountain ridges of increasing height. In the lower mountain districts wheat is grown on the plateaux, in the higher mountains wheat is grown in the valleys and on the slopes up to a height of 1,200 m.

No important physical barriers separate the Netherlands from the neighbouring countries. From the point of view of wind-borne cereal diseases North-west Europe can be seen as one great wheat growing district with many microclimates, bordered by the Atlantic in the west and by the Pyrenees, the Mediterranean and the Alps in the south. To the east and the north the physical boundaries are of a different kind, being a continental climate to the east and a boreal climate to the north.

It must be emphasized that none of these boundaries can be regarded as absolute, as has been shown by recent studies in black rust *(Puccinia graminis)* epidemiology. Black rust inoculum for example can by-pass the Pyrenees in its long journey from the Iberean Peninsula to England, being carried over the Bay of Biscay (OGILVIE & THORPE, 1958). Regions north of the Alps such as the Swiss plains and southern Germany share in the European black rust pandemic, which is supposed to start in Mediterranean regions and which goes northwards up to the Netherlands and England. With regard to brown rust *(Puccinia recondita)* French observations indicate that the Mediterranean is not a very effective boundary between North Africa and southern France (CHEVALIER).

12 WHEAT AND WHEAT CULTURE

12.1 The wheat plant

As the living green parts of the wheat plant are the substrate supporting the yellow rust, we must pay some attention to the wheat plant and the wheat culture. The available studies on wheat cannot completely satisfy the pathologist.

Therefore some complementary investigations have been carried out by the writer.

12.11 Normal crop, codification of growth stages

The normal wheat plant has been the subject of many publications and does not need an elaborate discussion. For the codification of the different growth stages the FEEKES scale (FEEKES, 1941) has been used in the version of LARGE (1954), see table 12.11 and fig. 12.11. The advantages of this scale were twofold: it was detailed and it could be applied by the residential and the travelling observer at any time, even during flying visits, contrary to the much used system for residential observers in which the dates of specified events as the heading or flowering are noted. The time interval between the different FEEKES-stages is variable.

The FEEKES-stages of the young plant were too widely spaced in time for the present investigation, especially in the case of winter wheat. In the stages 2 to 9 a subdivision has sometimes been used, the first figure marking the FEEKES-stage, the second figure recording the number of tillers formed and the third indicating the number of leaves per plant. With both numbers the figure 9 means nine or more tillers or leaves per plant.

The leaves of the growth stages 1 to 4 will be called "seedling leaves". The leaves developing during the growth stages 5 to 7, the transition stages between tillering and shooting, will be called "transition leaves". After shooting the seedling leaves have died. The transition leaves are now at the foot of the wheat

TABLE 12.11 Growth stages in cereals: FEEKES scale, emended by LARGE

Growth stage GS		
1	One shoot (number of leaves can be added) = "brairding"	Tillering
2	Beginning of tillering	
3	Tillers formed, leaves often twisted spirally. In some varieties of winter wheat, plants may be "creeping" or prostrate	
4	Beginning of the erection of the pseudo-stem, leaf sheaths beginning to lengthen	
5	Pseudo-stem (formed by sheaths of leaves) strongly erected	
6	First node of stem visible at base of shoot	Stem Extension
7	Second node of stem formed, next-to-last leaf just visible	
8	Last leaf visible, but still rolled up, ear beginning to swell	
9	Ligule of last leaf just visible	
10	Sheath of last leaf completely grown out, ear swollen but not yet visible	
10.1	First ears just visible (awns just showing in barley, ear escaping through split of sheath in wheat or oats)	Heading
10.2	Quarter of heading process completed	
10.3	Half of heading process completed	
10.4	Three-quarters of heading process completed	
10.5	All ears out of sheath	
10.5.1	Beginning of flowering (wheat)	Flowering (wheat)
10.5.2	Flowering complete to top of ear	
10.5.3	Flowering over at base of ear	
10.5.4	Flowering over, kernel watery ripe	
11.1	Milky ripe	Ripening
11.2	Mealy ripe, contents of kernel soft but dry	
11.3	Kernel hard (difficult to divide by thumbnail)	
11.4	Ripe for cutting. Straw dead	

plant and accordingly they will be called "foot leaves". The latest leaves are the "stem leaves".

The main stem of Heines VII plants normally has four stem leaves, the total number of leaves along the main tiller varying from nine to fifteen. Early secondary stems have four stem leaves. The number of tillers per stool is variable according to sowing rate, soil fertility and other factors. In volunteer plants high numbers of tillers can be found. On the other hand volunteers of spring wheat in wintertime may be in the boot stage, having only one stem with three living leaves. The Feekes-scale and its additions permit a description in code of many different forms of the wheat plant, see examples in 16.

12.12 Late tillers

At the time of tillering numerous buds sprout to give fertile and grain rendering tillers, many dying in the contest for space and light; however several buds remain dormant. Under special conditions some of these may sprout later in the season to give rise to late tillers which may flower but do not set grains. According to the time of development of the late tillers we distinguish pre-harvest and post-harvest late tillers.

Pre-harvest late tillers are not frequent. They can be found on the borders of fields and in open places. These late tillers are smaller than normal tillers, generally having two or three stem leaves which at harvest time stand out as green flags among the yellow ripening crop. Their frequency on bordersides varies from 1 per 10 meter to 1 per 100 meter border length. Most of them are mowed off or at least partially mowed off during harvest, but occasionally one escapes the cutting knife. The number of such escapes per field can be counted mostly on the fingers of one hand.

The cutting of insufficiently ripened plants may give these plants an impulse

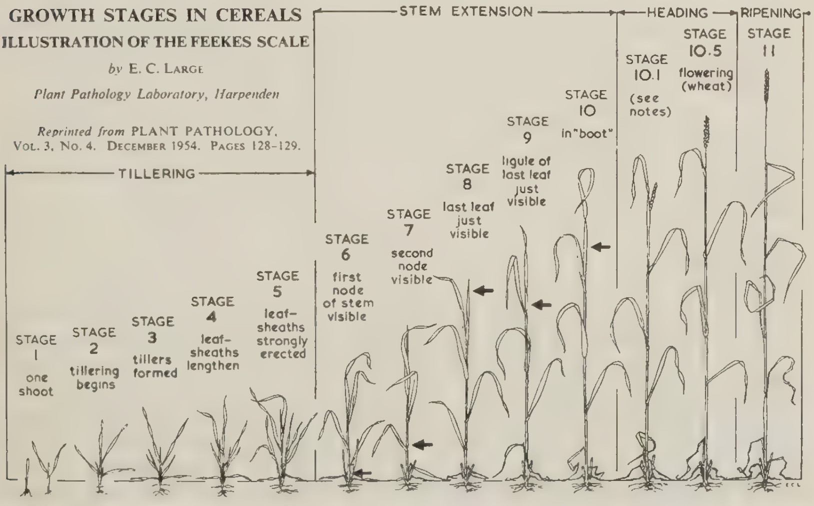


Fig. 12.11 The Feekes scale for the codification of the growth stage GS as illustrated by Large.

to renewed sprouting or to further development of small green sprouts already present before harvesting. Post-harvest late tillers (synonymous with ratoon tillers: Joshi, 1957) can be found on the borders and on wet patches of a field. The number of post-harvest late tillers can be considerable, varying from 1 in 100 sq.m. to 1 in 1 sq.m. Normally the formation of many late tillers is a local event due to wet soil, overdose of nitrogen or too early mowing. In wet summers the phenomenon is more general. The highest frequency of late tillers observed was 1 per sq.m. Example: Heines VII / Ilpendam/7162/25–9/D 7–10/IV/ +(c.1 /sq.m). Varietal differences in the capacity of late tiller formation may exist.

12.13 Self-sown plants

After harvesting self-sown plants become apparent. To these volunteer plants the same division in pre-harvest and post- harvest must be applied. Pre-harvest volunteer plants generally appear in clusters. Their origin is due to summer storms. Heavy rain or hail sweep stems to the bottom when the kernels are milky or mealy ripe. The grains being not yet in their dormancy sprout immediately and give rise to the pre-harvest volunteer clusters. At the time of harvesting, leaves in such clusters are 3 to 5 cm. long. Pre-harvest volunteer clusters are rare, the highest frequency observed being about 1 per 100 sq.m.

The grains shed by the wind and by the harvest procedures give rise to a crop of post-harvest volunteer plants. 100 plants per sq.m. is quite normal, 1,000 plants per sq.m. is not exceptional. Occasionally a farmer is so content with his volunteer crop that he maintains it as an early sown production crop for the next season. The frequency of pre- and post-harvest volunteer plants is largely determined by weather conditions; it is high when there is much rain in the two weeks before and after the harvest, it is low in dry summers, as in 1959.

12.14 Adventive wheat

This category contains those forms of wheat which do not fit into one of the former categories. Adventive wheat occurs on or near dung and rubbish heaps, barns and threshing places. It may also occur on road sides. Volunteers of a second generation, growing for example in a potato crop are also called 'adventives'.

The phenomenon of adventive wheat is rare. A few plants on the off-side of a barn or near a refuse heap are all which can be found. Adventive barley, on the other hand, is quite frequent especially on road sides, but it is also found in potato crops.

12.2 Aspects of the wheat culture

12.21 Types of wheat

The two main types of wheat are winter wheat, with a long vegetation period and spring wheat with a short vegetation period. In Scandinavia the sowing dates of winter and spring wheat are separated by an interval of a half-year. Further southwards the sowing dates can overlap as in the Netherlands, where the spring wheat Peko occasionally is sown early in January, two weeks before the latest sowing of the winter wheat Cappelle (Haarlemmermeerpolder, 1958).

In the Mediterranean region sowing dates depend on local climate, altitude and water supply. At the lower altitudes only winter wheat is sown, which often has a short vegetation period.

Harvesting dates of winter wheat and spring wheat are not so widely seperated as sowing dates. Spring wheat is harvested from a few days up to a few weeks later than winter wheat.

12.22 Wheat-free period and residual wheat

Important to epidemiology is the wheat-free period; this is the period from harvest time of the spring wheat until sowing time of the winter wheat. The length of the wheat-free period has been mapped in map 12.22. Information on sowing dates is derived from the observation forms of the International Yellow Rust Trials and from an inquiry by the Netherlands Grain-Centre. Harvesting dates have been copied from the inquiry mentioned above or have been computed by extrapolation methods from the International Yellow Rust Trials. The length of the wheat-free period is given as the number of decades between the harvest of spring wheat, or winter wheat when no spring wheat was recorded, and the sowing of winter wheat. To cover the period between sowing and emergence one to two decades should be added to the data presented in map 12.22.

The map shows a marked gradient from south to north; in the Mediterranean region a wheat-free period counts 100 to 200 days; in Scotland and Scandinavia it is only 0 to 30 days. Negative values have not been recorded, but may occur in central Sweden and in the high Alps. In Eriksson's time negative values up to –30 days were frequent in the Stockholm area. Aberrant low values in Spain, southern Germany and Austria are due to high altitude observations.

The wheat-free period is the period during which no commercial wheat crop is grown. This does not mean that the period is entirely free from wheat as there may be a residue of late tillers and volunteers. The amount of residual wheat varies according to local conditions.

This phenomenon of residual wheat is bound up with climate. It appears only in regions with summer rainfall. So the phenomenon is limited to the Atlantic zones of North-west Europe as in the Netherlands and Belgium, and to some mountainous regions as in Switzerland. In regions with a more continental climate such as central Europe or central Spain and in the Mediterranean zone there is hardly room for the phenomenon discussed. In these regions it is so hot that the wheat ripens evenly without late tillers and it is so dry that no volunteers can germinate during summertime.

12.23 Cultural methods

In 12.1 it has already been explained that the so-called wheat-free period is not always free from wheat. Late tillers and self-sown plants make up a certain quantity of residual wheat. Apart from the climatic factors already mentioned, cultural methods determine the amount of residual wheat in summer time. Cultural methods are of paramount importance in regions where the climate permits the growth of large amounts of residual wheat, as in the Netherlands.

Before the advent of tractors, weedkillers and shortage of labour, the stubble fields of good Dutch farmers were ploughed over and over several times during the summer and autumn. With such procedures any residual wheat could be eradicated before the emergence of the next wheat crop. In modern times manpower and tractor capacity are needed in the potato campaign which starts shortly after the wheat harvest and in the subsequent beet campaign. The time available for ploughing in the stubble is restricted and often the fields are

shallowly ploughed or cultivated once during summer and deep ploughed in late autumn, long after the emergence of the new winter wheat crop.

Special practices may complicate the general picture. In the Netherlands the undersowing of a clover crop as green manure is in general use; Yellow Trefoil *(Medicago lupulina)*, sown in spring and ploughed in in the late autumn, is widely used. Incidentally White Clover replaces Yellow Trefoil. Red Clover is also used though not frequently. A Red Clover crop will be maintained as a green fodder or hay crop during the next season. When the clover crops are well developed the self-sown wheat has few chances for development. Quite often however the clover crops are poor and give room to an abundant growth of volunteer wheat.

12.24 Regional differentiation

Local differences in the Netherlands add to the variation. In the Oldambt in East-Groningen wheat is the main crop and wheat fields are well cared for. In the "Hoekse Waard" in the province of Zuid-Holland consumption potatoes are the main crop and little attention is paid to the wheat fields after harvest. In the district of Zuid-Limburg the sowing of wheat is one month or more later than in the rest of the Netherlands, as it is a general practice in this region to sow the winter wheat after sugar beet.

On the light soils of the Dutch and Belgian coastal region deep ploughing is postponed to the spring and this practice is in special favour in the seed potato growing district of Friesland, where deeply loosened light soils are essential for the growing of a high quality product. On the light soils of Belgian Flanders the wheat stubbles sometimes remain untouched until early spring.

In northern France (departments Nord, Pas de Calais, Somme, Aisne, Oise) there is a mosaic pattern of large and small fields. The large fields, belonging to estates measuring hundreds of hectares, are well cared for. The stubbles are ploughed in late summer or early autumn. The small plots belong to small holders, not mechanised and living in villages sometimes far from the fields. Their stubble fields are often untouched until spring, then manured and ploughed. Large numbers of volunteers may grow on these small plots.

There is little evidence of ecological niches where green wheat plants can oversummer, protected from the plough. In the Netherlands with its many ditches such niches could be formed by ditch walls. Careful inspection however did not reveal any wheat plant in the thick grass growth of ditch sides. Apparently the wheat gets little chance for germination and further development in the rough turf. In the shade of barns and on or near refuse heaps occasional wheat plants can be found. It might be supposed, that in hot countries, as for example in Spain, irrigation ditches and mountain stream valleys require consideration. However, during a short visit to Spain the writer found no confirmation for this supposition. The irrigation ditches were either clean or presented a thick grass growth which makes germination of wheat improbable. The mountain stream valleys were idyllic, but they were often far from the wheat fields. It must be admitted, that the search for volunteer plants in Spain was not extensive.

13 THE RUST FUNGUS

13.1 The name

SCHMIDT described yellow rust on glumes in 1818 under the name *Uredo*

glumarum. FRIES in 1821 used the specific name *glumarum* in *Trichobasis glumarum*. In 1854 WESTENDORP, *médecin de bataillon au 12me régiment de ligne*, described yellow rust under the name *Puccinia striaeformis*; FUCKEL in 1860 gave it the name *Puccinia straminis*. ERIKSSON & HENNING in 1896 introduced the name *Puccinia glumarum*. This name was held in esteem until recently HYLANDER, JØRSTAD & NANNFELDT (1953), followed by CUMMINS & STEVENSON (1956) and MANNERS (1960), revived the name *Puccinia striiformis* Westend., which is the valid name for the yellow rust fungus. In the American literature "yellow rust" is usually called "stripe rust".

Yellow rust forms uredospores abundantly. Teleutospores are found frequently on several hosts, wheat included. According to the literature the teleutospores germinate readily (ERIKSSON & HENNING, 1896). No alternate host of yellow rust is known. In the future the alternate host might be found, but so far as we know the yellow rust fungus lives quite comfortably without an alternate host. *Puccinia striiformis* should be included in the hemicyclic rusts.

The morphology of the fungus has been described in great detail (ERIKSSON & HENNING, 1896; VIENNOT-BOURGIN, 1940–41). In the following paragraphs the yellow rust will be depicted as a disease with clear though variable symptoms, as it is seen by the pathologist.

Yellow rust occurs in all continents except in Australia. The rust occurs in many climates but shows preference for the cooler and moister coast and mountain regions.

13.2 Symptoms on seedlings in the greenhouse

In typical cases a yellow rust lesion on the primary leaf is a yellow fleck, covering the width of the leaf and measuring several centimeters in length, composed of numerous small pustules which sporulate abundantly. The pustules are approximately spindle shaped, often arranged in lines between and on the veins of the leaf. They are about one half mm. in length, and rather variable in shape. The broken epidermis is not conspicuous. The pustules, closely crowded together, shed many spores which cover the green surface between the pustules.

On the tip and base edges of the lesion a zone of lighter green, measuring up to half a cm. in width, is sometimes present. On the border of the sporulating lesion and the light green zone an area with closed pustules can sometimes be seen. On the lower side of the leaf pustules are often smaller and more widely scattered.

In the greenhouse, when light is short, the pustules will remain smaller and spaced more widely. In intermediate cases the pustules have the normal dimensions, but are arranged in alternating pustule free and sporulating bands of about 3 mm. wide. This band phase, which in the greenhouse is often seen in certain race-host combinations, is a temporary phase in lesion development.

With the increasing resistance of the host varieties the dimension of the pustules decrease, and more and more chlorotic patches appear. In fully resistant host plants no reaction at all occurs after inoculation or the reaction consists of chlorotic flecks, sometimes with a few small unopened pustules or necrotic dots. Small and large pustules, light and intensive chlorosis and necrotic flecks can occur in many combinations, either evenly distributed over the whole lesion or divided into a mosaic pattern.

13.3 Symptoms on seedlings and mature plants in the field

In the field the symptoms on the primary leaf and the lower three to five leaves are the same as in the greenhouse. Lesions may begin as oval flecks measuring 0.5 to 1 cm., varying in colour from a light discoloration of the normal green to violent yellow chlorosis. These flecks are frequent in periods with extreme temperatures, either cold or hot. After some days pustules will appear in the centre of the fleck, which under less extreme conditions enlarges rapidly.

On the transition leaves the lesions start in the same way as on the seedling leaves. Sometimes transversal growth of the lesions is stopped by a vein, which apparently cannot be penetrated. The resulting symptoms are stripes from 1 to 10 mm. broad. If after all a vein is penetrated by the fungus the lesion acquires an irregular rectangular shape.

On the stem leaves the stripes are narrow, generally they are not more than 1 or 2 mm. wide. The pustules, not different from those of the primary leaf, lie in lines. On both ends of the stripe a zone of light green or yellow may be seen. The stripes measure from a few millimeters up to c. 10 cm. long. The length of the stripes depends on the number of lesions per leaf, the age of the infection, and the environmental conditions during growth. Sporulation on the lower side of the leaves is often less intense than on the upper side.

Typical stripes sporulate abundantly. The sporulating leaf is very susceptible to adverse weather conditions. The lesions turn chlorotic and necrotic when it is either too wet, too hot or too dry. When normal conditions return the stripe can continue its growth on one or both ends. The chlorotic part does not turn green again, it may however sporulate for a few days under conditions of high humidity. When the leaf is severely infected the lesions sometimes can be grouped into age groups differing in the degree of chlorosis and necrosis and in the freshness of the pustules. These groups indicate different outbreaks, they reflect different infection periods.

Lesions often occur on the sheaths of the leaves. They sporulate only on the inside of the sheaths. Lesions on the stem are relatively rare in wheat. As on the sheaths they are extremely narrow but sometimes up to 5 cm. long. The writer, however, has never seen sporulating lesions on the wheat stem. Fields, severely attacked by yellow rust and sporulating on the stems, have been reported by SANTIAGO from Portugal. The same can be seen on some very susceptible barley varieties, e.g. Topper.

Uredosori on the heads are frequent. They can occur on all green parts of the heads, especially on the glumes, which sporulate on the inside only. The young kernels can be covered with a thick layer of uredospores. ERIKSSON & HENNING (1896) and HUNGERFORD (1923b) report endo-uredinia from the seed coat of the green kernel.

Teleutosori occur on the leaves, the sheaths, the stems, the glumes, the rachis and the awns. On the leaves they are minute stripelets arranged in the same pattern of longitudinal lesions as the uredosori. Teleutosori are very conspicuous, when on the sheaths, stems and awns they alternate with uredosori, forming a fine pattern of black and orange dots.

In the field mature plants attacked by yellow rust are characterized by their yellow discoloration and dryish appearance with upright folded leaves. Attacked

fields can be recognized by their foci or yellow patches of heavily affected plants. Severely attacked fields can be detected by their yellow colour and dryish appearance. In the early stages of shooting and after heading the wheat can be nearly defoliated. The drills in the shooting period have a particular profile, the two or three younger and more or less green leaves standing out as a plume, the lower leaves already shrivelled.

The aspect of an infected field is quite variable. In the transition stage a 100% infected layer of lower leaves can be destroyed by heavy rain, leaving a seemingly rust-free crop. In the shooting stage a severely rusted field can temporarily look green when a new layer of leaves appears. It is at this stage that optimistic farmers think that the threat of rust is over. Vigourously sporulating leaves of clear orange colour have a dull yellow tint after a thorough wash by rain. The brightness of the yellow colour in the early morning fades away as the sun gains in strength.

13.4 Codification of infection types for greenhouse work

As the original classification of the infection types by Gassner and Straib (1932) was too detailed, in the present investigation a simplified classification has been used (conform Fuchs, 1960):

i = no symptoms,
0 = chlorosis and/or necrosis, no pustules,
1 = chlorosis and/or necrosis, pustules small and few in number,
2 = chlorosis, little or no necrosis, few small pustules,
3 = chlorosis, many large and abundantly sporulating pustules,
4 = no chlorosis, many large and abundantly sporulating pustules.

Infection types are indicated by arabic figures, instead of the more clumsy roman figures, usual in rust work.

When the leaf did not show the same type over the whole surface gradual variations were indicated by the symbols 0-2, 0–4 and 2–4. Sometimes the leaves showed patches with chlorosis alternating with type 4 patches. This was indicated by the codes 2+4 and 0+4. A young infection of the future type 4 can be confused with a type 1 infection. A young type 4 was coded $4^{=}$. Type 4 reactions but with a few small chlorotic flecks (c. 2 mm.) probably due to light deficiency were coded 4.

Webster often showed a special reaction where the rust lesion developed into a type 4 lesion though with rather small pustules; then the pustules turned brown and died and the lesion became a modified type 2 lesion. This reaction, also found in a few other varieties such as Hybrid 46, was called the Webster reaction and was indicated by the codes 2w, 4w etc.

13.5 Codification of infection types for field work

Throughout this work the International Scale for the recording of infection types in the field has been used. This scale was drawn up in 1956 by the First International Yellow Rust Conference in Braunschweig, Germany. It is practically the same scale as the one used for the recording of infection types in the greenhouse.

International scale:

i = no attack
0 = no pustules, only chlorosis (c = small areas, C = large areas),
1 = some separated, very small pustules and also chlorosis (c, C) or necrosis (n, N),
2 = a few pustules, also chlorosis (c, C),
3 = normal pustule formation, also chlorosis,
4 = normal pustule formation, without chlorosis.

Type reading in the field is more difficult than in the greenhouse, as the reaction types may be complex and variable. For detailed description double codes (e.g. 2 +4) and intermediate codes (e.g. 0–2) can be used. As a type 4 reaction may turn necrotic after one hot day remaining recognisable as a dead type 4, codes as 4N have been used.

The type assessment can be made from an individual leaf, a stem, a plant, a hassock or a field, and should represent the average value of the infection type on the object to be assessed.

13.6 Codification of the degree of attack for field work

Most European breeders use a scale from 0 to 5, 5 denoting absence of rust. The pathologist prefers scales in which the grades go up with increasing amounts of rust, they also prefer a more detailed scale. The scale should be used for epidemiologic observations as well as for the comparison of varieties. The scale should be adapted to the layman's use. Therefore the intervals of the scale have to be clear. For example a different between 5 and 10% of leaf surface attacked can be seen easily, the equally large difference between 50% and 55% of leaf surface attacked can hardly be observed.

These contradicting requirements have been met by the International Scale, accepted by the First International Yellow Rust Conference. On the writer's suggestion the lower part of the scale (grades 1 to 4) was adapted to epidemiologic observations, the scale values forming a logarithmic progression. The upper part of the scale (grades 4 to 10) is well adapted for variety comparison.

International Scale:

0 = no infection observed
1 = one lesion to 10 metres drill length
2 = one lesion to 1 metre drill length
3 = one lesion to 0.1 metre drill length
4 = at least one lesion to the tiller, but no more than 1% of leaf surface attacked
5 = 5% of leaf surface attacked
6 = 10% of leaf surface attacked
7 = 25% of leaf surface attacked
8 = 50% of leaf surface attacked
9 = 75% of leaf surface attacked
10 = 100% of leaf surface attacked

The symbol + has been used in this publication to indicate that rust was recorded without mention of the degree of infection. Mostly the actual degree of attack was low. Any infection of yellow rust with one lesion to ten metres drill length or less has been coded as 1.

In case of doubt, advice was given to take a sample of three to ten well developed stems. The percentage of the leaf surface attacked by yellow rust was estimated leaf for leaf. For every stem the leaf percentages were averaged to a stem average. The stem averages were combined into a sample average. This sample average was rounded off to the nearest percentage of the International Scale and the corresponding degree of attack (DA) was noted.

The DA of the ears has often been noted separately. The same International Scale was used, only instead of "leaf", "glume" should be read.

Standard diagrams for the estimation of the intensity of yellow rust infection have been drawn by MANNERS (1950), reproduced in the instruction booklet for the observation of the International Yellow Rust Trials, and by SALAZAR (1954).

14 TECHNIQUES IN HANDLING YELLOW RUST

14.1 Routine techniques in the greenhouse

Plants were grown in a semi-conditioned greenhouse at temperatures varying from 18° to 22°C. Ten to fifteen seeds per pot with an upper diameter of 10 cm. were sown. When the primary leaf was unfolded smaller and abnormal plants were eliminated until some six good plants remained. When necessary plants were stored in the cold room at 2°C. with continuous light for three days at the most. The varieties Michigan Amber and *Triticum dicoccum tricoccum* have been used for the multiplication of inoculum.

Inoculations were done in a special inoculation cage, which before and after each inoculation was disinfected by spraying a fine and dense mist of tap water through the cage for some minutes. Several inoculation methods have been tried. Rubbing a well sporulating leaf against the leaves to be infected was the most convenient method for routine work. A good technician could inoculate eight to twelve leaves with one sporulating leaf. In routine work a one to four proportion was normal.

Before inoculation the wetted leaves were drawn between thumb and index finger to remove the wax layer. A characteristic soft, peeping noise was thought to indicate the right pressure of the fingers. This procedure makes small droplets adhere better to the leaf surface. After inoculation the leaves were sprayed with a fine mist of tap water. In later work, however, both procedures were omitted without apparent loss of infections.

Inoculated plants were kept under polyethylene plastic cages in a conditioned greenhouse with temperatures of 15° ± 3°C. During the first days after inoculation the cages were closed to keep the relative humidity at 100%. On the third day the cages were opened until sporulation began; this occurred at about the tenth to forteenth day after inoculation. Then the cages were closed again except for a narrow slit.

The resulting low humidity checked the growth of secondary fungi on the inoculated leaves.

Solar irradiation could heighten the temperature in the plastic covers with 5°C. or more, but even during a dark dreary wintry day the temperature in the cages is about 1°C. higher than between the cages. This was avoided by hanging a fine muslin gauze in the greenhouse some 20 cm. above the cages. The loss of light in the plastic cages was the same as in glass cages.

On the sixth day after inoculation the developing shoot was cut off, leaving

only the inoculated leaf. When necessary this procedure was repeated on the twelfth day.

Other methods of inoculation were tried. Inoculation with a brush, either wet or dry, was succesful but not better than the rubbing method. When the amount of inoculum was small a scalpel was used for inoculation. With this instrument one or a few uredosori could be picked up and transferred to another leaf.

The cyclone method (TERVET, 1951a, b; MACER) was adapted to the yellow rust work and found satisfactory for the collection of spores. Under normal conditions spores can be collected three times with two-day intervals. The collector is disinfected by immersion in 70% alcohol. Mass inoculation, using the cyclone to produce a spore cloud, was not practiced in routine work.

14.2 Unipustular cultures

During his stay at the Institute for Phytopathological Research (I.P.O.) in Wageningen in 1957, WAHL adapted the technique of unipustular cultures to yellow rust work. On the edge of a young lesion a pustule was chosen, above which the epidermis did not show more than a narrow slit. Care was taken to select a young pustule from a zone, where no scattered spores were visible at hand lens inspection. The chosen pustule was cut out with a safety razorblade. With a pair of tweezers the isolated pustule was rubbed over the leaf to be inoculated.

In routine work six leaves per pot were inoculated with six separate pustules. When the first yellow rust chlorosis was visible on a leaf, the other five leaves were cut off to prevent the mixing of spores descending from different pustules. The use of unipustular cultures was a safe and convenient method to purify isolates; about 70 % of unipustular inoculations is successful.

The use of unipustular cultures in yellow rust work was mentioned first by BECKER (1933).

14.3 Light conditions in the greenhouse

In the Netherlands light can be a growth limiting factor, especially in greenhouses where only 30 to 70 % of the total outside radiation is transmitted by the windows. As solar irradiation contributes greatly to warming up a greenhouse, the conditioned greenhouse was whitewashed in order to keep the temperature within limits. This method resulted in a good temperature but led frequently to light deficiency. The symptoms of this deficiency, though clear, were only recognized in a late stage of the work. Light deficiency, which makes yellow rust work impossible during the winter, has still a marked effect in April and October and may occur during dark periods in midsummer as for example in August, 1960. Identification data from light deficient periods have to be discarded. During a dark and sunless fog period of six weeks in the winter 1958–59 dozens of isolates got lost.

The symptoms of light deficiency may be arranged in four groups:

1. Top chlorosis of the primary leaf, appearing about one week after emergence or later,
2. escapes from infection, the percentage of i-type readings rising from the normal 10 % level up to 50 % or more,
3. irregularity of infection, reaction types varying greatly between i and the expected value,

4. average infection type (escapes excluded) lower than the expected value, the test variety being Michigan Amber with an expected value of 4.

After finding the cause of the trouble, artificial illumination was increased up to the technical limits. Daylength was kept constant at 15 hours a day, except in midsummer, when the natural daylength was up to 17 hours. The lamps used were fluorescent tubes Philips W'TL'F colour 33 alone or together with high pressure mercury vapour bulbs Philips HPL. Light intensity was measured with a spherical radiation meter (WASSINK & VAN DER SCHEER, 1951) on plant height, 10 cm. above pot soil level. The unit of measurement is 1,000 $erg.sec^{-1}.cm^{-2}$ sphere diameter. Results are listed in table 14.3.

TABLE 14.3 Light intensities in the greenhouse

place of measurement	temp. in °C	plants in plastic cages	daylight noon 28–9–60		lamp light
outside greenhouse	.	.	565	100%	.
inside greenhouse					
between benches	.	.	185	33%	.
compartment 9	18	—	74	13%	47
compartment 2L	15	+	52	9%	45
compartment 2R	15	+	85	15%	9
compartment 3	15	—	117	21%	35
,,	15	+	.	.	9

The unit of light intensity is 1,000 $erg.sec^{-1}.cm^{-2}$ sphere diameter.
For explanations see text.

For purposes of comparison, measurements of sunlight intensity have been taken on 28th September, 1960, at noon during sunshine, cloudiness 0.4. Lamplight has been measured at night. The data for lamplight provide the values of minimum light intensity, as normally daylight adds to the total light intensity during part of the daily irradiation period. All entries in table 14.3 are bench averages. The individual readings differ greatly according to position on bench, accidental or systematic shading, etc.

The difference "inside greenhouse, between benches" and "outside greenhouse" gives an impression of the light transmission by the greenhouse. Light intensity on benches is lower than between benches because of shading by lamp armatures. Inside the plastic cages light intensity may be still lower.

In compartment 9 plants are kept at c. 18°C. until the second leaf appears, this taking place about one week after emergence. In compartment 2 the rust isolates are maintained and inoculum is multiplied, every isolate kept separately in a plastic cage. During the first week after inoculation plants are kept on the high light intensity bench, for the second week on the low light intensity bench; this system was imposed by technical limitations. Cages rotate through the compartment in order to give them an approximately equal amount of light. Race identification is done in compartment 3, where plants are kept under plastic cover only for the first 48 hours after inoculation.

14.4 The storage of isolates

The storage of the isolates was a problem. Originally all isolates collected or

received were kept alive by continuous cultivation. This procedure was unsatisfactory, not only because it made costly greenhouse space unproductive but also because of the risks of losing an isolate during winter, of introducing impurities into the isolate, or of interchanging etiquettes, risks which are proportional to the number of transfers.

The risk of losing an isolate by the failure of an inoculation was diminished by keeping fresh sporulating leaves of the same isolate in corked tubes at 2 °C. in the cold room until the success of the inoculation was assured. In this way reserve material of an isolate could be maintained from two to six weeks.

Gassner & Straib (1932) advised storage of spores at 38 % relative humidity at about +1 °C. s'Jacob (I.P.O., Wageningen) found this method to be unsatisfactory. Storage under vacuum was suggested to the writer by Macer (Plant Breeding Institute, Cambridge). Cylindrical ampoules of 6 mm. ø were used. In the middle a constriction of 0.3 × 2 cm. was made. Spores and talcum powder were collected in this ampoule, attached to the cyclone collector, and then mixed. The ampoules were attached to a support and evacuated over phosphorous pentoxyde over a period of six hours at room temperature. The residual air pressure was about 0.5 mm. Hg. The ampoules were melted off at the constriction, controlled for vacuum with a high frequency vacuum tester and stored, in the beginning at room temperature, later in a refrigerator at +2 °C. The continuous cultivation of the isolate was stopped when at least five ampoules from at least three different collection days had been stored.

During the first year of experimentation 70 % of the ampoules gave a succesful inoculation after storage times varying from 1 to 350 days. Several isolates got lost, but on the whole this method was more satisfying than continuous cultivation with its great demand of labour and of greenhouse bench area and its many risks. In the future technical perfection will reduce losses to a minimum.

14.5 Rust nurseries

Apart from some special experiments described elsewhere, the field work consisted of rust nurseries for variety comparison or race characterization.

Spore suspensions in tap water or in 0.1 % agar have been used for field inoculations. Spores were taken from greenhouse cultures, vacuum ampoules or from the infected plants in the field. The spore suspension was sprayed over the plants with a De Villbiss number 15 atomizer. The inoculated plants were covered with a pot for 48 hours to keep humidity high. The rubbing method, applied in the greenhouse, was less succesful in the field, but was sometimes used in winter.

Rust nurseries were of great help in this investigation. The succes of rust nurseries depends mainly on two factors: the relative amount of highly susceptible varieties and the earliness of the field inoculation. The rust nurseries are sown in hassocks with help of the tube method (Hendriksen & Wieten, 1954). The proportion of susceptible varieties to varieties to be tested should be at least one to five.

As spreader variety any of the highly susceptible varieties Little Club, Michigan Amber, Michigan Bronce, Persian, Harvest Queen, Redman or Rubis can be used. The writer generally used Michigan Amber which is universally susceptible to all rust races tested. The disadvantage of an universally susceptible variety is that on such a host one race or isolate may outgrow the other isolates.

Though the field may be inoculated with a number of isolates it is then in fact tested against one isolate only. Such dominance, first mentioned by s'JACOB (1956), cannot be recognized without appropriate differential varieties.

Differential varieties can be used instead of universally susceptible varieties. These varieties are highly susceptible to one race or race group. Each differential variety is inoculated with its compatible rust isolates. The further development of the isolate can be followed and its virulence under given environmental conditions can be assessed. In the Wageningen rust nursery the writer used a dual system, in which part of the spreader hassocks was made up of universally susceptible varieties. Even then only one race may become dominant, for reasons as yet not understood.

14.6 Race nurseries

Special mention must be made of race nurseries. These nurseries give detailed information on the reaction of a collection of varieties to one chosen isolate. Race nurseries require special attention regarding isolation and inoculation.

To prevent the invasion of unwanted rust from the outside, good isolation is necessary. In the village of Baarn race nurseries were established, where a nurseryman was growing ornamental trees (yellow rust trials 3671–3679). Three to four nurseries were sown every year on distances of at least 50 m. The isolation by this distance and by the high shrubs was satisfactory, as shown by the reaction of the specific control varieties. No commercial wheat is grown in a radius of 10 km. around Baarn.

In 1957, when the yellow rust epidemic was severe and occurred very early, two of the three race nurseries in Baarn were already invaded by the rust before inoculation had taken place. So it would appear that, even under optimal conditions of isolation, race nurseries are unreliable in years with high epidemic activity of the rust.

The capacity of Baarn being too small, another solution had to be found. With the help of the Zuiderzeepolders Development and Colonization Authority *(Directie van de Wieringermeer)* 60 small race nurseries were sown in the new polder Oostelijk Flevoland (season 1959–60). The race nurseries were established in a 30 ha. field of winter swede rape. The minimum distance between the nurseries was 64 m. In all growth stages the rape was much higher than the wheat. Adjoining the trial field were lucerne and winter swede rape fields. The minimum distance between the nurseries and the commercial wheat fields was 900 m.

Regularity of infection was assured by a large proportion of spreader hassocks, being one third to one half of the total number of hassocks. As far as possible differential varieties were used as spreader varieties, all spreader hassocks belonging to one variety.

The inoculation had to be effected at an early date, when possible in March. A nursery was inoculated on at least ten hassocks and at least two different times. The inoculum for the accessory inoculations was grown in the glasshouse or taken from the spreader varieties of the race nurseries.

15 THE INTERNATIONAL YELLOW RUST TRIALS PROJECT

15.1 Objectives

The International Yellow Rust Trials Project comprises the sowing and ob-

servation of variety trials in many places in and outside Europe. The initiative was taken by the Committee for Yellow Rust Research in the autumn of 1955. The execution of the project has been entrusted to the writer.

The International Yellow Rust Trials Project was designed to collect information on the following problems:

1. the epidemiology of yellow rust,
2. the physiologic specialization of the yellow rust,
3. the behaviour of resistant and susceptible varieties tested under different environmental conditions.

The Yellow Rust Trials were also meant to distribute resistant parents. Several breeders used the resistant parents provided in their breeding programme.

The writer was charged with the preparation and expedition of the seeds for the yellow rust trials, the collection and evaluation of the observations and the personal control by visit. The *Biologische Bundesanstalt* (Braunschweig, Germany) has taken an important share in the work by accepting yellow rust samples from all trials for identification.

15.2 The varieties

The varieties for the Yellow Rust Trials were chosen to meet the requirements of the problems stated above. The varieties can be classified into four groups:

1. Susceptible varieties
   These varieties are highly susceptible to yellow rust under all conditions tested. They permit the study of epidemiology, being indicative of the level of infection in the neighbourhood of the trial. Furthermore they are thought to pick up and multiply inoculum so that contiguous varieties of the trial will be infected.
2. Commercial varieties
   Commercial varieties have been included to establish a link between the Yellow Rust Trials and the commercial wheat culture. One or more characteristic and widely used varieties were chosen from nearly every North-west European country.
3. Differential varieties
   Several varieties were tried for their capacity to differentiate yellow rust races or race groups. For differentiating purposes commercial varieties were preferred to 'museum' varieties without agricultural value.
4. Resistant varieties
   Several varieties or breeders lines with conspicuous resistance to yellow rust have been tried with the purpose of detecting hidden rust races, which for some reason cannot be discovered on the normal varieties.

Some of the varieties used were pure lines, especially the French varieties. Other varieties belonged to the category of the "pooled varieties", being a mixture of lines descending from one cross. Some Swedish, German and Dutch varieties belong to this category. The mixture can be a consequence of a not too rigid selection or of a deliberate mixture of a few selected pure lines. In the case of pooled varieties attention must be paid to the question whether or not the different lines of the mixture differ in rust reaction.

When possible the starting seed material for the Yellow Rust Trials was certified seed. After introduction this seed has been multiplied from year to year

in the Netherlands. Originally it was thought sufficient to apply a severe negative mass selection in order to maintain the purity of the seed. This procedure however proved to be inadequate. So it was decided to change over to line selection, a change not yet completed when this treatise was written.

The use of pure lines has the advantage of a very restricted genetical variability. The disadvantage lies in the possibility of choosing the wrong line. The risk of choosing a line not representative for the reaction of the variety can be diminished by carefully testing several lines for the reactions wanted and choosing the line with the most adequate reactions. The actual process of narrowing down the genetical variability of a pooled variety or of an impure variety to that of a pure line variety should be accompanied by extensive tests in the greenhouse and in the race nurseries in order to ensure a correct choice of the line.

Varietal purity is ensured by mass selection and ear selection, isolation of the multiplication plots in rye or winter swede rape, transport and storage of the unthreshed straw in sacks and alternate threshing of wheat varieties and barley or rye. These methods have been introduced gradually, but it is too early to report on the results.

The number of varieties to be used in the Yellow Rust Trials is limited, so that the trials should not consume too much of the observer's time. A careful inspection of the trial should not take more than one to three quarters of an hour. To meet this requirement the number of varieties should not exceed thirty. For purely epidemiologic purposes a more restricted number of varieties was found to be sufficient. This led to the use of complete trials with 25 to 40 varieties and reduced trials with 12 to 16 varieties.

15.3 The trials

The location of the trials was strictly limited to those breeders, institutes, schools, experimental farms and advisory services who wished to co-operate, and were fully able to do so. In this way it was possible to cover many countries and many ecological situations. The pattern of the trials on the map (map 11.3.a, b and c) however remains very irregular, showing for example a great concentration of trials in the Netherlands. In this respect the Yellow Rust Trials Project as a uniform sampling method for sampling yellow rust in Europe is still defective.

The trials were sown according to instructions; these were to sow every variety in two drills of one meter length at 20 to 25 cm. distance. Some stations used hassocks (German: *Ofenröhre*) sown with the tube method instead of drills. The trials were located either in experimental fields or in farmers' fields. Sometimes the writer asked a station to sow the trial in a field of some special variety, in order to study problems of specialization of the rust.

As sowing time, the normal sowing time for the region was advised, since abnormal sowing times and sowing time experiments had little value for the investigations at this stage. Spring wheat had to be sown in spring to avoid the winter risks. However, no obvious differences between autumn sown and spring sown spring wheats were observed. Spring sown winter wheat often reacted quite differently from autumn sown winter wheat. Vernalised spring sown winter wheat also reacted differently from normal sown not vernalised winter wheat.

Chemical weed eradication and in general any spraying had to be avoided in and around the Yellow Rust Trial.

Some stations infected their experimental fields artificially with one or more

rust races. This practice complicated the epidemiologic evaluation of the data from the trial involved. On the other hand the study of physiologic specialization was greatly advanced by this very same practice.

Sometimes the trials were severely damaged by floods, birds, snails, mice or frost (winter 1956). Advice was given to keep the trial, damaged as it may have been. As long as one good plant of every variety remains, the data from the trial can be used.

15.4 The observations

The observations comprised the assessment of the growth stage, the type of infection and the degree of infection as described in the foregoing and in an instruction booklet sent to all observers of the Yellow Rust Trials. The observations were noted down on an observation blank together with the name of the station, the name of the observer, the date of the observation, sowing dates of the varieties and other relevant remarks. The observation form had to be despatched immediately to enable control by the writer. When the discrepancies of the observations received with other data were marked, the writer sometimes asked for leaf and ear samples in order to control the observations and the identity of the varieties, or he decided to go out to make a personal inspection. In this way many errors could be eliminated.

The stations were supposed to inspect their trial every week until the finding of the first yellow rust pustules. Subsequently, fortnightly observation was sufficient. The stations were asked to send yellow rust samples to the *Biologische Bundesanstalt* in Braunschweig (Germany), especially when the yellow rust made its first appearance and when differential or resistant varieties were attacked.

The instructions of the instruction booklet were kept short. This resulted in a many different interpretations. Most difficulties of interpretation could be resolved after personal contact with the writer, who travelled all over Western Europe establishing personal relations with the observers, especially in the first years of the Yellow Rust Trials. This activity led to a marked improvement of the observations and to greater uniformity.

16 FIELD WORK

A good deal of time was spent on field work. A field visit can be anything between a glance of a few seconds in cases with high degrees of attack, and a careful inspection of a couple of hours. Field work was done at any time of the year, and special trips have been made for the study of overwintering and oversummering.

Field notes consisted of the following items:

Variety	? = unknown	
Locality	Outside the Netherlands, country added between brackets	
Field number	First figure corresponding with the year of observation	
Date of observation		
Type of plants	No letter	= normal crop
	L	= preharvest late tillers
	R	= postharvest late tillers
	V	= volunteer plants
	A	= adventive plants

Growth stage
Type of attack
Degree of attack When foci were apparent their DA was noted separately with preceding F, attack of ears was also noted with DA following an E.

Other relevant remarks were written down, sowing date, exposition, manuring, estimated number of volunteers etc.

Examples:

Heines VII/Oostende (Belgium)/7326/10–7/11.1 /4 N/8 F 10 E 4 (rare)
L 10.52/2 /+

Heines VII, July 10th, 1957, near Oostende (Belgium), normal crop in milky ripe stage, type 4 attack but highly necrotic, at an average 50 % of the leaf surface infected but foci infected up to 100 %, light infection of the heads with about one lesion per ear, late tillers rare, in early flowering stage with a few type 2 infections.

Peko/N.O.P./8591/3–12/V 8.1.3/2 C/1 (1 plant in 10 sq.m.)

Volunteer plants of Peko spring wheat in the Noordoostpolder, visited December 3rd, 1958, plants in shooting stage, generally only one stem with three leaves per plant, type 2 infection with heavy chlorosis, few plants infected, estimated number of plants about 1,000 per ha.

2 PHYSIOLOGIC SPECIALIZATION AND EPIDEMIOLOGY

21 TERMINOLOGY

As the reader will become deeply involved in host-parasite relations, a clear idea of the terminology used is necessary. The following definitions are given in terms of variety and race, but these may be replaced by words indicating other taxa.

"Variety" is used in the agronomic, not in the taxonomic sense, the word being preferred to the less usual term "cultivar". A wheat variety is a more or less uniform and stable taxon, purposely selected or bred, remaining constant because of the self-fertilizing capacity of wheat and the continued selection of the breeder.

A rust race is an entity, distinguished from similar entities by major differences in reaction on a standard differential set. Sub-races can be distinguished by major differences on additional differentials. The distinction between races and sub-races is more a matter of convention than of biologic significance, as it depends only on the varietal composition of the internationally accepted standard differential set.

"Compatibility" characterizes the race-variety interaction. A race-variety combination is compatible, when it produces disease symptoms. As a race-variety relation can be anything between highly compatible and highly incompatible, compatibility can be looked upon as a quantitative character, to be

measured in terms of infection type IT or percentage of infection PA. Race R is compatible to variety A and incompatible to variety B, means the same as: variety A is susceptible and variety B is resistant to race R, or: race R is virulent to variety A and avirulent to variety B, or: variety A is compatible and variety B is incompatible to race R. The word compatibility is especially useful in studies on the influence of environmental conditions on race variety interactions, when it is not known whether the variety, the race or the interaction is sensitive to changes.

"Resistance" is "the sum total of qualities of the host which oppose the development of a given pathogen" (WILBRINK, 1940). Resistance and its opposite, susceptibility are quantitative characteristics of a variety; resistance can vary from extreme resistance to the utter lack of resistance, or, in other words, susceptibility can vary from absence of susceptibility to extreme susceptibility. This chapter deals partly with the problem of how to express resistance and susceptibility accurately in figures. Two forms of resistance will be distinguished, race specific and race non-specific resistance.

Race specific resistance is a form of resistance, which is active against one race or a definite number of races only. Most of this chapter deals with race specific resistance. Race specific resistance can be broad or narrow, according to the number of races to which the resistance is effective. "Broad race specific resistance" of a variety is analogous to "versatility" of a race. The broadness of the race specific resistance is a measurable quantity.

Race non-specific resistance is a form of resistance, which is active against all races of the pathogen. It will be dealt with in 25.3.

"Pathogenicity" is a character of the rust race, the analogue of resistance in the variety. It is the "ability to cause disease" (COMMITTEE, 1940). As in resistance, in pathogenicity two forms of pathogenicity may be distinguished, variety specific and variety non-specific pathogenicity. Variety non-specific pathogenicity, a concept comparable to the "aggressivity" and the "infectiousness" of GÄUMANN (1945), is of no importance in yellow rust work. Variety specific pathogenicity has two aspects, virulence and versatility.

"Virulence" and "avirulence" are characteristics of a race, referring to its relation with one specific variety. The word virulence is used to indicate the "relative capacity to cause disease; the degree or measure of pathogenicity" (COMMITTEE, 1940). Virulence is variety specific; the word virulence is analogous to "race specific resistance". A race is virulent to a susceptible variety (compatibility), avirulent to a resistant variety (incompatibility). Virulence can be regarded as a quantitative character, but it is difficult to measure this character.

"Versatility" is a character of a race, referring to its relation with a specified set of varieties. A race, which is virulent to many varieties of the set, is more versatile than a race which is virulent to a few varieties only. In a former paper (ZADOKS, 1959) the writer has inaptly named "aggressive", what is called "versatile" in this work. The word versatile has senior rights (LEVINE & BASILE, 1959). Versatility, too, can be regarded as a quantitative characteristic. A "versatile race" is analogous to a "variety with broad race specific resistance".

When a race is tested on a differential set, each differential responds in its own way. The reactions of the differentials together form a "reaction spectrum", which characterizes the race.

When a variety is tested with a set of races, this variety reacts to each race in a

typical way. The reactions of one variety together form a "reaction pattern", which characterizes the genetic make-up of the host.

The suitability of a variety to be used as a differential depends on two characters, "discriminative ability" and "homogeneity of response". By "discriminative ability" is meant the capacity of the variety to react with either a 0 or a 4 type; by "homogeneity of response" is meant the ability of the variety to react with the same infection type in all inoculated plants. Selkirk for example is undiscriminative but usually homogeneous, Hybrid 46 is sometimes very discriminative, but never homogeneous in its response.

22 YELLOW RUST ON GRASSES

22.1 Generalities

ERIKSSON (1894) distinguished five *formae speciales: f.sp. agropyri, elymi, hordei, secalis* and *tritici*; these have been cited in the handbooks ever since. ERIKSSON & HENNING (1896) mention only the *f.sp. hordei, secalis* and *tritici*. Few experiments have been done with the *f.sp. secalis*, none with the *f.sp. elymi*. ERIKSSON (1894) knew already that some *formae speciales* were more strictly specialized than others.

The epidemiologist has to investigate whether grasses act as accessory hosts of wheat rust or not. Two lines of approach are open:

1. a thorough field inspection of grasses to find out which grasses are infected, where, when and to what degree of attack (DA),
2. a testing programme to find out to what extent yellow rust is specialized on the generic level.

The student of epidemiology should start with isolates, taken from full grown, naturally infected grasses. In the greenhouse these isolates can be tested for specialization with the conventional techniques, using seedlings. This is emphasized, because some scientists (i.a. HASSEBRAUK, 1933; STRAIB, 1936c, 1939a) tested isolates from wheat on a large range of grass species in the seedling stage. Such experiments do not help in finding the solution to the problem of the epidemiologist, for the following reasons:

1. seedlings do not generally give the same reaction as mature plants (25),
2. growth conditions of the host and infection conditions in the greenhouse may differ greatly from those in the field,
3. intraspecific variation in the susceptibility of grass species may occur according to the strain, clone or provenance (see remarks by STRAIB, 1939a; BECKER & HART, 1939 and MANNERS, 1950).

In the greenhouse the isolates can be tested for specialization in the usual way. Conclusions, based on this technique are usually accepted as epidemiologic evidence. Generally speaking this acceptance is not justified, as the seedling may react quite differently from the mature plant, being in many cases more susceptible. Full epidemiologic evidence can be obtained only by inoculating race nurseries with isolates from grasses, but this has never been done.

22.2 F.sp. agropyri

Isolate 8894 from *Agropyrum repens* has been tested several times on *A. repens*, barley, *Dactylis glomerata* and wheat. Inoculations in the greenhouse were

TABLE 22.2.3 Inoculation results with isolates from grasses; greenhouse tests on seedlings; entries are infection types.

field number	provenance	wheat: Michigan Amber	wheat: *Trit. dic. tric.*	barley: Fong Tien	barley: Atlas	*Agropyrum repens*: A	*Agropyrum repens*: B	*Agropyrum repens*: C	*Agropyrum repens*: D	*Agropyrum repens*: NOP	*Dactylis glomerata*	rye: Petkus spring	rye: Petkus winter
TABLE 22.2 Isolates from *Agropyrum repens*													
8894	Noordoostpolder	4	4	3–4	i+4	i	i	i+0	i	2	i	i	i
0097	Noordoostpolder	.	.	i+4	.	i	2	i–1	i–0	i	.	.	.
TABLE 22.3 Isolates from *Dactylis glomerata*													
83041	Douai (France)	0N	.	.	0N	0N	.	.	.	.	4	.	.
83601	Westmaas	i	.	.	i	i	.	.	.	.	4	.	.
0100	Oostel. Flevoland	.	i	i	.	i	i	.	.	i	4	.	.

successful on the clone of *A. repens*, from which the rust had been isolated, on the seedlings of the exotic barley Fong Tien and of several wheat varieties (tables 22.2, A.23.25.b). Two commercial barley varieties, Atlas and Dea, showed one sporulating leaf each.

Susceptible and resistant strains of *A. repens* were encountered also by STRAIB (1939a, b) and MANNERS (1950). The three *Agropyrum* isolates of MANNERS did not infect any wheat or barley tested, except for the exotics Fong Tien and *Triticum dicoccum tricoccum*, these data being in accordance with those of STRAIB. VIENNOT-BOURGIN (1934) tested French isolates from *A. repens* on wheat, barley, rye and *A. repens*; inoculation was successful on *A. repens* only. BECKER & HART (1939) found isolates, similar to those of VIENNOT-BOURGIN in two localities.

Furthermore, BECKER & HART made isolates, which infected commercial barley varieties, from four different foci on *A. caninum*. From one focus on *A. caninum* they isolated race 6, a wheat race. BROEKHUIZEN (1955) collected yellow rust on *A. cristatum* at Wageningen; in Braunschweig the isolate was identified as race B 2x.

Generalizing on the basis of the evidence from several French isolates (VIENNOT-BOURGIN, STRAIB), six German isolates (BECKER & HART), three English isolates (MANNERS) and two Dutch isolates, it may be concluded that at least two races widely differing in their versatility seem to live on *Agropyrum* species. Whether the more versatile races also infect mature plants of commercially grown wheat and barley is not known. The designation *f. sp. agropyri* seems to be still useful, once the versatility of some of its races is recognized.

The epidemiologic evidence supports the conclusion of specialized forms on *Agropyrum*. The isolates 8894 (race W 6) and 0097, found on *A. repens* in the Noordoostpolder, came from two small foci in the road-side turf. The foci, each possibly formed by a susceptible clone, measured approximately 2 × 10 m.; they were separated by a distance of about 800 m. One focus was found at nearly each visit during the years 1958, 1959 and 1960. The rust overwintered in the focus, as sporulating leaves were found in the winter months too. The infection reached its maximum usually in September; stem leaves were infected

up to IT = 2 and DA = 5. There is no clear relation between the foci on *Agropyrum* and the yellow rust epidemics on wheat and barley in the Noordoostpolder. Certainly the amount of inoculum on *Agropyrum* was too small to be responsible for these epidemics.

22.3 F.sp. dactylidis

Yellow rust on *Dactylis glomerata* is a general occurrence in North-west Europe. Several isolates from Northern France and from the Netherlands have been tested in the greenhouse. The isolates grew well on seedlings of *D.glomerata*, but not on *A.repens*, barley or wheat (table 22.3).

These experiments corroborate the results of MANNERS (1950) and MASTENBROEK (1946). Yellow rust on *Dactylis* is highly specialized. To the pathologist the designation *f.sp. dactylidis* is fully justified. The taxonomist goes even further, promoting this form to varietal rank on the basis of morphologic arguments and on physiologic arguments apart from specialization: *Puccinia striiformis* WESTENDORP var. *dactylidis* MANNERS (1960).

The yellow rust epidemics on *D.glomerata* attain their maximum in August and September. Mature plants are infected and on susceptible selections stems and glumes may be covered with pustules. In road side plants a certain percentage, usually small, is found to be infected up to IT = 4 and DA = 8. *Dactylis* epidemics bear no relation to epidemics on wheat or barley, *D.glomerata* remaining free of yellow rust during severe epidemics on wheat or barley and being sometimes appreciably infected in a region without wheat or barley yellow rust.

22.4 F.sp. hordei

Yellow rust on barley is a common occurrence in the Netherlands. Several isolates have been tested; none of these infected *A.repens*, *D.glomerata* or wheat. These findings are in accordance with those of VIENNOT-BOURGIN (1934), STRAIB (1939a, b) and MANNERS (1950). They justify the use of the designation *f.sp. hordei*.

The writer isolated *f.sp. hordei* from several grasses out of his rust nursery (table 22.4). Consequently, the *f.sp. hordei* is not so highly specialized as the *f.sp. dactylidis*.

The highly specialized races 33 from *H.murinum* (STRAIB, 1939a) and M from *H.marinum* (MANNERS, 1950) deserve special mention; these seem to have a more restricted host range than some of those races frequenting commercially grown barley. This is in accordance with the findings of VIENNOT-BOURGIN (1934), who tested isolates from *H.murinum* on wheat, barley and *H.murinum*, and obtained infection on *H.murinum* only. In the Netherlands no yellow rust on *H.murinum* has been observed.

The best argument for the distinction of the *f.spp. hordei* and *tritici* is to be found in field observations. In the Netherlands, near the end of the growing season it often happens that the barley section of a variety trial is severely infected by yellow rust, whilst the wheat section remains practically free and vice versa. The grasses surrounding these trials, *D.glomerata* and *A.repens* inclusive, were in such situations always free from yellow rust. The only exception is a trial field in Oostelijk Flevoland, where *D.glomerata* was also infected, but this exception is easily explained, because road and ditch-sides in

Table 22.4 Yellow rust on grasses in the rust nursery, Wageningen, 1958

grass species		observations: GS/IT/DA 25-7-'58	7-8-'58	*f.sp.*
Aegilops caudata		–	–	
crassa		–	–	
ovata		–	–	
speltoïdes		–	–	
triticoïdes		–	–	
ventricosa		–	–	
Agropyrum caninum		10.52/2/3	11.1/3/7	*H*
cristatum		–	–	
smithii		–	–	
tenerum		–	–	
Arrhenaterum elatius		–	–	
Brachypodium sylvaticum		–	10.51/4/2	*H*
Bromus erectus		–	–	
macrostachys		–	–	
ramosus		–	–	
rubens		10.53/2/2	11.2/2/3	*T*
secalinus		–	–	
sitchensis		7-10.1/2/3	11.1/2/2	*T*
Briza media		–	–	
Castella tuberculata		–	–	
Dactylis glomerata	1	–	–	
	2	–	–	
	3	–	–	
	4	–	–	
	5	–	–	
	6	–	–	
	7	–	–	
Elymus canadiensis		–	–	
virginicus		8/2/3	8/3/3	*H*

grass species		observations: GS/IT/DA 25-7-'58	7-8-'58	*f.sp.*
Festuca pratensis	1	–	–	
	2	–	–	
	3	–	–	
	4	–	–	
rubra		–	–	
Haynaldia villosa		5/1/2	5/2/3	
Hordeum bulbosum		–	–	
jubatum		5(10.1)/2/2	10.54/3/2	*H*
nodosum		–	–	
Hystrix patula		–	–	
Lolium multiflorum	1	–	–	
	2	–	–	
	3	–	–	
mult. var. westerwoldicum		–	–	
perenne	1	–	–	
	2	–	–	
	3	–	–	
	4	–	–	
	5	–	–	
	6	–	–	
remotum		–	11.1/4/1	
rigidum		–	–	
Phleum pratense	1	–	–	
	2	–	–	
	3	–	–	
	4	–	–	
Poa pratensis	1	–	–	
	2	–	–	
	3	–	–	

Seed samples have been kindly provided by:
Dr. I. Wahl, Faculty of Agriculture, Rehovot, Israel,
Kon. Kweekbedrijf en Zaadhandel D. J. van der Have N.V., Kapelle-Biezelinge.
grass species: numbers are different samples
– = no yellow rust observed
f.sp. = *forma specialis*, *H* = *hordei*, *T* = *tritici*

this new polder were sown with a mixture of grasses, among which was a high percentage of *D. glomerata*, susceptible to the *f.sp. dactylidis*.

22.5 F.sp. tritici

Isolates from wheat, as far as tested in the greenhouse, did not infect *A. repens*, barley or *D. glomerata*, with the exception of the exotic and highly susceptible barley Fong Tien. These results, in accordance with those of Viennot-Bourgin (1934), Straib (1939a) and Manners (1950), justify the designation *f.sp. tritici*.

Again, *f.sp. tritici* is not so highly specialized that it never infects other gramineae than wheat. In the International Yellow Rust Trials mature plants of the barley Topper, highly susceptible to the *f.sp. hordei*, are frequently infected with the *f.sp. tritici*, up to a DA = 4. This infection on the mature plant has been reproduced in the greenhouse.

Isolate 8894 from a focus in the Noordoostpolder behaved like wheat race W 6 (table A.23.25.b). It infected one out of four *Agropyrum* strains tested, the strain from which it was isolated. In a race nursery at Baarn, inoculated with the virulent race W 13, a plant of *A. repens* showed a type 2 lesion. In one of the race nurseries in Oostelijk Flevoland, also inoculated with race W 13, yellow rust was found on a few leaves of *Puccinellia distans*; isolates from both grasses were identified as race W 13. In some race nurseries in Oostelijk Flevoland *Puccinellia distans* was infected on the stems, where moderately sporulating pustules developed. No greenhouse experiments were made, but it is not too hazardous to attribute this infection to wheat rust. Several grasses in the Wageningen rust nursery were found to be infected by wheat rust, as identified in the greenhouse (table 22.4); IT and DA of these grasses were low.

Several authors mention wheat rust isolated from grasses. Except for the data of BECKER & HART (1939) no details of the conditions of infection and the severity of the attack were provided. STRAIB (1939a) isolated wheat rust races from *Bromus tectorum* and *Hordeum jubatum* (Braunschweig region, Germany). BECKER & HART isolated race 6 from a large focus on *A. caninum* near Ilfeld (Germany). BATTS (1957a) found wheat rust on *Festuca scoparia* (England) and BROEKHUIZEN (1955) isolated wheat rust from *Agropyrum cristatum*.

22.6 The danger of yellow rust on grasses to the wheat culture

As a rule, grasses seem to be frequented by their own special forms, which do not infect commercially grown wheat varieties in the mature plant stage. Occasionally grasses are found to be infected by the *f.sp. tritici*. Several of the examples, contributed by the writer, could be traced to the abnormal conditions present in rust nurseries. Reviewing the European literature only the reference of BECKER & HART (1939) to a large focus of wheat rust on grass has been found. The writer's isolate 8894, however, infects the primary leaves of several wheat and barley varieties.

In appreciating the danger to the wheat culture to be expected from yellow rust on grasses, and on *Agropyrum* especially, five points must be considered:

1. yellow rust is highly specialized on the generic level, with a few notable exceptions on *Agropyrum* species. These exceptions can be partly traced to a minority of clones, susceptible to the *f.sp. agropyri*, and a still smaller minority susceptible to the *f.sp. tritici*.
2. The growth rhythm of yellow rust on *Agropyrum* is different from that on wheat, the rust on *Agropyrum* coming later to its maximum development (ERIKSSON, 1894; 22.2).
3. The amount of inoculum on *Agropyrum* at the onset of a wheat rust epidemic is small, compared to the amount of inoculum on the wheat itself.
4. Field observations showed, that the *f.spp. hordei* and *tritici* can overwinter and oversummer on barley and wheat more easily and in larger amounts than on *Agropyrum* (33).
5. The writer made about 10,000 field visits in a period of five years. At each visit the grasses passed in going from car to field, and the grasses within the crop have been swiftly inspected. Yellow rust on *Dactylis* was relatively frequent in northern France, Belgium and the Netherlands. Yellow rust on *Agropyrum* was, however, extremely rare, two foci having been found in the Netherlands (22.2), one focus in Switzerland (1957) and one infected leaf in Sweden (1956).

In view of these arguments it is concluded that yellow rust on grasses is of little or no importance to the wheat culture. This conclusion is thought to be valid for the Netherlands and probably also for the larger area of North-west Europe.

23 RACE IDENTIFICATION IN THE GREENHOUSE

23.1 The Braunschweig work

Several German scientists studied physiologic specialization of yellow rust before GASSNER & STRAIB (1933) working in Braunschweig, Germany, introduced the differential set, which is still widely used. This set consists of the following varieties:

1. Michigan Amber 29-1-1-1
2. Vilmorin Blé rouge d'Écosse
3. Strubes Dickkopf
4. Webster C.I. 3780
5. Holzapfels Frühweizen
6. Vilmorin 23
7. Heines Kolben
8. Carstens Dickkopf V
9. Spaldings prolific
10. Chinese 166
11. Rouge prolifique barbu

The last two varieties were at that time regarded as accessory differentials. Today they belong to the standard differential set.

These eleven differentials have been chosen by GASSNER & STRAIB out of 1,400 varieties on one criterium only, their discriminative ability. They served well to differentiate the races known in 1932. Their symptom expression was as stable and their discriminative ability as large as could be found. Whether the resulting classification showed any relation to field phenomena was not a major consideration.

Main conditions for testing were:

1. average temperature of 15°C with a maximum daily variation of ± 3°C,
2. relative humidity about 80 % (the first 3 days 100 %),
3. plenty of daylight without direct solar irradiation.

Plants were grown 8 to 10 in 8 cm. ø pots in a greenhouse at 18° to 20°C., such plants having long leaves and showing regular infection. At the time of inoculation they were given 5 ml. of an 1.5 % ammonium nitrate solution. Inoculum, grown on Michigan Amber, was transferred with a cotton brush, wetted in 0.1 % agar solution. Inoculation was carried out, when the second leaf appeared. In summer time greenhouse cooling was difficult, so the identification season ran from October till May.

A rust isolate was cultivated on Michigan Amber until it was free from brown rust, mildew and other undesirable fungi. The purified isolate, called population, was used for preliminary differentiation tests. Concurrently, at least three monospore cultures were prepared from the population, which were also tested. In 1933 GASSNER & STRAIB published a list of 14 races, identified with the above mentioned 11 differentials.

TABLE 23.1 The short Braunschweig key for the identification of yellow rust races (FUCHS, 1960). Greenhouse tests on seedlings; entries are infection types.

differentials / races	1 Michigan Amber	2 Blé rouge d'Ecosse	3 Strubes Dickkopf	4 Webster	5 Holzapfels Frühweizen	6 Vilmorin 23	7 Heines Kolben	8 Carstens V	9 Spaldings prolific	10 Chinese 166	11 Rouge prolifique barbu	Heines VII	Cappelle	Vilmorin 27	Frontana	Reichersberg 42
1x	4	4	4	2–4	4	4	4	2–4	i–0	i–0	i–0	2–4	4	2–4	4	0
55	4	4	4	2–4	4	4	0	2–4	i–0	i–0	i–0	0–4	4	4	4	0
2x	4	4	4	2–4	4	4	0	2–4	0–4	i–0	0–4	2–4	4	2–4	4	0
17/26	4	4	4	2–4	2–4	0	0	4	2–4	i–0	0–2	2–4	0	0+	0+	0
5/6	4	4	4	2–4	2–4	0	0	0–4	0+	i–0	0+	0–2	0	0	0+	0
7/8	4	4	4	0+	2–4	0	0	0–4	0+	i–0	0+	4	0	0	0	0
$7xV_1$	4	4	4	0+	2–4	0+	0	4	4	i–0	2–4	2–4	0	0+	0	0
7x	4	4	4	0+	2–4	0	0	4	0+	i–0	0+	4	0	0	0–4	0
7A	4	4	4	0+	2–4	0	0	2–4	0	i–0	0	4	0	0	0	4
54	4	4	4	0–2	2–4	0	4	2–4	0–2	i–0	0–2	2–4	0	0	4	0
27/53	4	4	4	0–4	2–4	0	0	4	0–4	4	0	2–4	0	0+	0	0

As a result of war disturbances and of changes in staff after World War II there was a marked discontinuity in the yellow rust work. A new era began in 1955, when Dr. EVA FUCHS took over the yellow rust work in Braunschweig; at the same time a new interest arose in the Netherlands. Close co-operation was initiated at the First International Yellow Rust Conference in Braunschweig, February 1956. With the help of a few monospore cultures, remaining from pre-war work, FUCHS tried to revaluate the differentials and the race classification based on them. Her techniques were those of GASSNER & STRAIB, but with improved temperature regulation and irradiation. Identification proper was only done in spring and autumn.

In 1960 FUCHS produced a revaluation of the race classification (table 23.1). Many of the old races were classified into race groups, where differences between the races of a group were not sharp enough. Some of the current races happen to be clearly defined, others belonged to groups within which gradual transitions from one race to another could be observed. This grouping of races in what will be called "transition groups" is a new development in the history of yellow rust identification work.

23.2 Greenhouse work in Wageningen

The writer's objectives were the following:

1. to maintain a collection of samples from fields with a yellow rust infection of particular epidemiologic interest,
2. to find those differentials with which provisional information about an isolate could be obtained without the use of a large differential set and without tedious repetitions,
3. to compare seedling and mature plant reactions.

No extensive race testing programme was executed, as by agreement this task was delegated to the Braunschweig station. The *Biologische Bundesanstalt* took care of the rust samples received from the International Yellow Rust Trials, and kindly gave special attention to samples of epidemiologic interest collected by the writer.

A good deal of time was lost in obtaining the necessary know-how, finding out the best working conditions, balancing the exigency of a good working speed against the necessity of numerous repetitions; the working speed to obtain enough quantity, the repetitions to guarantee an acceptable quality of data. As a result only the data produced in 1960 and some data from 1959 are sufficiently reliable to be accepted as evidence.

Morphologic field studies of the differentials revealed some interesting points. One was impressed by the heterogeneity of each of the differential varieties, grown from seed, obtained by courtesy of the *Biologische Bundesanstalt* at the beginning of the work. None of the varieties was pure. Two ideas arose as a result of the morphologic observations: in the first place, it was necessary to apply a rigid selection and multiplication scheme (the attempted negative mass selection did not work); and in the second place, a detailed description of the differentials taking into account morphologic and physiologic characters, was needed to support the selection work. All stages of selection should be controlled in the greenhouse by exchanging type cultures of the rust races and seed samples of the varieties between the Braunschweig and Wageningen stations.

The work, described in the following pages, has been done with impure or partially purified varieties. The same holds good for the Braunschweig work up to the present time. Although the impurity of the differentials was a nuisance, it did not impede obtaining useful results.

A yellow rust sample was purified from brown rust and mildew by passing the isolate over Fong Tien barley or by picking up some yellow rust pustules with a broad needle after hand lens inspection. Technically such an isolate is still a sample of the original population and it may be composed of different races or biotypes. Actually this situation was never met; all populations behaved as pure races. This may be due in part to the sampling technique, as care was taken to sample mainly from those varieties which differentiate in the field. Partly it may be derived from the fact that two races are not likely to have identical growing speeds. It is more probable that one race outgrows the other, a process speeded up by the numerous transfers usually done in an early stage of sporulation. Thus, thanks to the semi-systemic growth of the yellow rust, "populations" can be used for routine identification work. Nevertheless it was customary to make unipustular cultures (14.2). Monospore cultures have not been used, but they might be needed in future work on race description and host-parasite-genetics.

Differentials were kept in plastic cages at 100 % RH during the first 2 days after inoculation, after this period the cages were removed and the plants were exposed to an average RH of about 80 %. Reaction types were read repeatedly with 2 to 3 days interval; the reaction of each leaf was separately recorded. Type reading and race identification were handled as two distinct actions. Type reading was done in the greenhouse and race identification was done in the office, using all the type readings produced and taking into account secondary knowledge, such as the relations between reaction types and general light

intensity, taking into account seasonal effects and impurity of the differentials. For identification the type readings of the 18th day were usually chosen.

Final judgment was based on trained feeling and not on the detailed calculations, as was suggested by LEVINE & BASILE (1959). To some this might seem to be more like a magician's than like a scientist's procedure. However, the system works, though improvement is badly needed.

23.3 Environmental conditions and compatibility

The body of knowledge on the effect of environment on compatibility is inversely proportional to the variability of the differentials, when the different wheat rusts are compared. As the yellow rust differentials are so variable, all information on this subject is valuable, even if this information is not based on specially designed experiments.

23.31 Temperature and compatibility

The main variable is the temperature, which has great influence on the compatibility reaction. The importance of temperature, expounded at length by GASSNER & STRAIB (1929, 1930a, 1933) and NEWTON & JOHNSON (1936) has been so generally recognized that all yellow rust identification work is done at 15° ± 3 °C. Variations of 3 °C. are allowed, when these are not of too long duration. Special care should be given to the temperature during the 48 hours following inoculation, when RH must be 100 %. There are indications that temperature during these two days has a decisive effect on the further development of infection (compare MOHAMED, 1960). Each race-differential combination reacts in its own way to changes in temperature, the general tendency being increased compatibility with decreasing temperature (GASSNER & STRAIB, 1933).

23.32 Relative humidity and compatibility

Next in importance is relative humidity. To obtain more information on this subject, two sets of data have been compared, identification results at 100 % RH (closed plastic cages) and at 80 % RH (no cages, daily average of RH about 80 %, the first two days excepted). Four races have been studied. The general tendency is increasing compatibility (increasing IT) with increasing RH. The effect varies with the race-variety combination. The main variable is the variety, the second variable is the race (table 23.32, details in table A.23.32). Strubes Dickkopf, Carstens V, Rouge Prolifique and Holzapfels Früh are rather sensitive to high RH.

The data presented are not unbiased. The 100 % series dates from 1959, the 80 % series from 1960. Though the races in the two series or years were the same, the isolates were sometimes different. The effect of the stepwise improving seed purity could not be excluded, as is demonstrated by the variety Chinese 166 in table A.23.32. Notwithstanding these bias, the comparison of the two series is suggestive. It confirms the statement of GASSNER & STRAIB (1933), who mentioned the same effect and even the same varieties. The contradictory statement of MANNERS (1950) is probably due to erroneous citation.

When insolation is intense the RH in the greenhouse becomes too low and reaction types change subsequently. Type 4 becomes 4N, 2–4 or 2N. Type 2 becomes 2N or 0N. Webster is especially susceptible to drought.

TABLE 23.32 Relation between compatibility and relative humidity RH in some differential-race combinations. The table indicates the increase of the compatibility of some race-variety combinations at c. 100% RH, compared to the compatibility at the normal testing RH = c. 80%. For details see table A.23.32.

differentials \ races		W 8	W 12	W 13	W 16
1	Michigan Amber	–	–	–	–
2	Blé rouge d'Écosse	++	++	++	+
3	Strubes Dickkopf	++	+	+++	+++
4	Webster	+	–	–	–
5	Holzapfels Frühweizen	++	++	++	++
6	Vilmorin 23	+	+	+++	+
7	Heines Kolben	–	+	+	+
8	Carstens V	+++	+++	+	+
9	Spaldings prolific	++	++	–	–
10	Chinese 166	.	.	–	++
11	Rouge prolifique barbu	++	++	++	+++

. = no data available
– = compatibility at 100% RH not increased
\+ = compatibility at 100% RH increased with 0.5 IT point
++ = compatibility at 100% RH increased with 1 IT point
+++ = compatibility at 100% RH increased with 2 IT points

23.33 Irradiation and compatibility

The third factor of concern is irradiation, a term preferred to the more usual "illumination". Irradiation, whether solar or artificial, must be adequate. Deficient irradiation leads to a decrease in compatibility, which does not necessarily express itself by lower infection types, but which often becomes apparent by a prolonged incubation time (see GASSNER & STRAIB, 1929; BEVER, 1934), a smaller number of pustules more widely spaced over the leaf surface, and a decreased sporulation (see 14.3). In more serious cases of light deficiency the inoculation is partly successful or even unsuccessful. A high percentage of i types is a warning signal. Some isolates and races are more susceptible than others to light deficiency. Varietal differences, too, seem to be operative. Failing responsiveness might be due in part to inadequate irradiation during the 48 hours following inoculation (see BEVER, 1934).

Light should be adequate during all three periods, the pre-inoculation period, the actual penetration period (48 hours at 100% RH), and the subsequent period until type reading. Experiments during the autumn of 1960 suggest the minimum level of irradiation to be between 30,000 and 50,000 ergs.sec^{-1}.cm^{-2} sphere ø, using fluorescent tubes alone or in combination with high pressure mercury fluorescent bulbs.

Daylength is a matter of importance too, as was demonstrated by BEVER (1934) and MANNERS (1950). Again it is Carstens V which is very sensitive to daylength. BEVER showed that a long day can change the reaction type from 4 to 0, compared with a short day. In the Wageningen experiments daylength was maintained at 15 hours, the average natural daylength over the summer half-year.

Direct solar irradiation has to be avoided. Several observations suggest insolation damage during the penetration period, a damage which becomes ap-

TABLE 23.33 Average difference between daily minimum and maximum temperature in closed plastic cages. The difference t between daily minimum and maximum temperature in a closed plastic cage was measured over several days; the values t of each experiment were averaged and the average $\bar{t}$ was entered in the table. Meteorological data were averaged over the same days as the temperature observations. The greenhouse temperature was 15° ± 3°C. The observations were done in June and July 1958.

Effect of variation in sunshine; light shading by greenhouse structures.

TABLE 23.33.a	C	R	$\bar{t}$	n
no sunshine	0.8	335	6.1	14
little sunshine	0.8	424	7.5	6
more sunshine	0.5	545	11.4	8

Effect of variation in shading by greenhouse structures

TABLE 23.33.b	C	R	$\bar{t}$	n
no shade	0.7	376	11.6	11
light shade			9.6	

Effect of variation in shading by a newspaper

TABLE 23.33.c	C	R	$\bar{t}$	n
no newspaper	0.8	333	9.2	8
newsp. 40 cm. above cage			6.5	8
newspaper close to cage			5.7	8

C = average daily cloudiness during daytime of observation days
R = average daily radiation in cal./sq.cm. of observation days
$\bar{t}$ = average difference between daily minimum and maximum temperature in °C.
n = number of temperature observations per entry

Meteorological data by courtesy of the Laboratory of Physics and Meteorology of the Agricultural University, Wageningen

parent by a deviation of the infection types from the expected values. Whether the damage is due to a light reaction near the leaf surface or to a temperature effect in the plastic cage is not known. Table 23.22.a shows the average difference between minimum and maximum temperatures in closed plastic cages during a period in June 1958, under conditions of variable sunshine and moderate shading. This difference can be more than 10°C., which means that without shading temperatures of over 25°C. are not infrequent in the plastic cages. Such high temperatures can change reaction types from 4 to 0 (NEWTON & JOHNSON, 1936). Table 23.33.b shows similar data for different points in the greenhouse, one with full insolation and one with partial shade by greenhouse structures. Table 23.33.c presents data on artificial shading with a newspaper. Shading by cheese cloth, which does not interfere with air circulation, has been adopted as a routine method.

23.34 Inoculum and compatibility

The inoculum should be grown under conditions of moderate temperature (approximately 15°C., GASSNER & STRAIB, 1930 a) and adequate irradiation

conditions (BEVER, 1934). No experiments have been done by the writer, but the general impression was gained that a poor quality of the inoculum influenced the identification results materially, mainly by causing high percentages of i types, but also by lengthening the incubation time by 1 to 3 days. There was no evidence that poor quality had an effect on the reaction type.

It is supposed that the poor quality of the inoculum has its main effect in the first days after inoculation, when the penetrating mycelium has not yet entered the host cells and is consequently dependent on the nutrient supply of the spore.

When an identification is done at Braunschweig and at Wageningen, both stations using the Braunschweig isolates and the Braunschweig seed, different results may be obtained. This not a matter of personal interpretation of reaction types, as Miss FUCHS and the writer ascertained during reciprocal visits. Minor differences in environmental conditions are supposed to be the cause of the difference. Detailed research is much needed, but can be done only in climate rooms excluding sunlight.

23.4 The standard differentials

As selections have been made from the original material, the Braunschweig selections will be characterized by adding -B, the Wageningen selections by adding -W to the names of the varieties. To compare the merits of the selections, tests were carried out with type isolates of some races. With each race all test plants were simultaneously inoculated. Results are presented in table 23.4.

1. Michigan Amber-W: The old stock of MA-B was highly susceptible in the greenhouse. In the field it was highly heterogeneous, moderately resistant to yellow rust, often lacking the characteristic violent red coloration on the stem at the onset of ripening. MA-W has been selected from seed kindly provided by VON ROSENSTIEL, Nordsaat G.m.b.H., Waterneverstorf, Germany. In the greenhouse MA-W is always susceptible, but the degree of compatibility seems to depend on the light intensity. In the field it is uniform, highly susceptible to yellow rust and other diseases (among which *Fusarium* is notable) and very susceptible to sprouting in the ear. In the greenhouse MA-W compares favourably to MA-B as regards reaction type and homogeneity of reaction.

2. Blé rouge d'Écosse-W: This selection is still impure. In the greenhouse BrE-W reacts approximately in the same way as BrE-B, the latter being more homogeneous. Neither of the selections is ideal, as they give too often reaction types lower than the expected value 4.

3. Strubes Dickkopf-W: A nearly pure selection, which in the greenhouse gives intermediate and rather variable reactions. SD-W is clearly less good than SD-B.

4. Webster-W: An interesting variety, in the beginning very inhomogeneous. The variety does not seem to be genetically instable as MANNERS (1950) suggested, but is probably freely cross-pollinating. In the greenhouse the reactions are variable, often intermediate, sometimes very trying, especially when pustules of young type 3 or 4 lesions turn brown and die. This is the Webster-reaction, often designated as type 2w. FUCHS' favourable impression of the critical capacity of Webster could not be corroborated in Wageningen. On the basis of field characters three lines have been selected. As yet no definite choice can be made. Multiplication of Webster is always difficult, as the multiplication rate is low. Sometimes plots have to be protected from mildew by Karathane. Of the

TABLE 23.4 A comparison between the Wageningen and the Braunschweig selections of the yellow rust differentials; greenhouse tests executed in Wageningen; entries are infection types.

date of inoculation, 1960	22–07	26–07	10–06	03–06	09–08	provenance of seed
provenance of isolates	W	B	B	B	B	
isolates	105	115	116	117	118	
races	B 27/53	B $7xV_1$	B 17/26	B 2x	B 55	
1 Michigan Amber	4	4	4	4	4	W
	4	4	2–4	2–4	2^{+}	B
2 Blé rouge d'Écosse	2–4	4	4	2–3	4	W
	2–4	4	4	3	4	B
3 Strubes Dickkopf	2	0–2	2–4	4	4	W
	4	4	4	4	4	B
4 Webster	2	2	$2^{\pm}$	0–4	2^{-}	W
	2	2	2	3–4	2^{+}	WA
	2^{-}	2^{-}	0	3^{-}	2	WB
	0^{+}	0–2	0	0–3	2	WC
	1–2	$2^{\pm}$	0	i–2	2+4	B
5 Holzapfels Früh	2^{-}	4	4^{-}	0–2	0+4	W
	2–4	2–4	4^{-}	0–3	4	B
6 Vilmorin 23	0^{+}	0^{+}	0	4	4	W
	2	0–2	$2^{\pm}$	$2^{\pm}$	4	B
7 Heines Kolben	0	0	0	0^{+}	$1^{\pm}$	W
	0	0	0	1–2	2	B
8 Carstens V	4	4	4	0	0	W
	4	4	4	0	0	B
9 Spaldings prolific	2^{-}	2^{+}	2^{+}	i	i	W
	2	i+4	2+4	i	i	B
10 Chinese 166	4	0	0	0	0	WA28
	4	0	0	0	0	WA48
	2–3	0	0	0	0	WA49
	4	0	0	0	0	WA75
	4	0	0	0	0	WB
	3–4	0	0	0	0	B
11 Rouge prolifique barbu	0–1	2^{+}	0	0	0	W
	0	2^{-}	1	i+0	0	B

Webster selections the mixture W-W is too variable, this applies also to W-B.

4A. Webster-WA: This awned line has the usual wax layer. The mature plants are moderately susceptible to yellow rust and highly susceptible to mildew.

4B. Webster-WB: This awned selection has also the usual wax layer. Mature plants are resistant to yellow rust and moderately susceptible to mildew. The selections W-WA and W-WB are more discriminative than the others and W-WA seems to be the most homogeneous, but the amount of data is still too small to make a decision which line is the best one.

5. Holzapfels Frühweizen-W: An impure selection, poorly differentiating, giving variable results and next to useless for identification work. HF-W seems

to be rather more discriminative and homogeneous than HF-B, but neither of them is very helpful.

6. Vilmorin 23-W: A pure selection and a good differential. V23-W compares favourably to V23-B in discriminative ability and homogeneity.

7. Heines Kolben-W: The original HK-B stock was a mixture of plants with red and yellow antheres. According to LEIN, the breeder of F. Heine Saatzucht-wirtschaft, Schnega, Germany, the type with the yellow antheres corresponds to the original type. This type has been used for testing. In the greenhouse HK has a good discriminative ability and homogeneity; it is one of the best differentials. HK-W compares favourably to HK-B.

8. Carstens Dickkopf V-W: Several lines of this variety exist, varying widely in their mature plant susceptibility. CV-W has mature plant resistance to most races, but moderate mature plant susceptibility to race W13. CV-W and CV-B seem to be equally good and show good discriminative ability, in striking contrast with the data of FUCHS (1960), where CV appears as a poor differential. MANNERS (1950) appreciated CV as a good differential.

9. Spaldings prolific-W: A fairly uniform selection of doubtful value for race identification. SP-W is less good than SP-B.

10. Chinese 166-W: LEIN stated that the field aspect was different from the original material, which he had used in hybridization work at Halle (Germany). Apparently the change in exterior morphology did not affect the behaviour of Chinese 166 as a differential variety. The old Ch-B stock was quite heterogeneous in the field, with many resistant types. In the greenhouse the old material, which should be resistant to every race except race W13, showed 20 % of susceptible plants, these having broad leaves in marked contrast to the narrow leaves of the other 80 %. Two selections have been made. Though their differences in the greenhouse are small, the selection Ch-WA is obviously the better one.

10A. Chinese 166-WA: Mature plants are only susceptible to race W13; they are fairly resistant to mildew. In the greenhouse the selections Ch-WA_{28}, Ch-WA_{48} and Ch-WA_{75} compare favourably to Ch-B.

10B. Chinese 166-WB: Mature plants generally susceptible to yellow rust and moderately susceptible to mildew. In the greenhouse the reaction of Ch-WB is good.

11. Rouge prolifique barbu-W: This selection does not seem to be of much use for race identification under Wageningen conditions; this applies to Rpb-B also.

Cross-pollination in wheat is not infrequent. Estimates vary from 5 % in normal years to 10 % in exceptional years (DANTUMA). In some of the differentials, especially in Webster but also in Chinese 166, this percentage seems to be much higher. Therefore multiplication is done in small plots, isolated by 5 m. broad screens of winter swede rape, which reaches approximately 1.50 m. high at the flowering time of the wheat. It cannot yet be established with certainty in how far this isolation is efficient.

The ultimate aim of the selection work is to find good pure lines. The varieties, as tested in 1960, were roughly speaking halfway through the selection process. When pure line material was not yet available, a seed mixture from field selected ears has been used. Other selections were already pure lines. The diffi-

culties due to impurity of the seed material will be overcome within a few years, and then full agreement can also be reached between the Braunschweig and Wageningen stations regarding the pure lines to be used for identification work.

23.5 Other varieties tested in the greenhouse

Apart from the differentials about 40 varieties have been tested. In all cases work has been done with selections which are supposed to be representative for the varieties in morphologic and physiologic qualities. To distinguish the Wageningen selections from the commercially grown seed the suffix -W has been added to the names of the varieties.

The varieties tested can be divided into three groups (FUCHS, 1960), viz.:

1. supporting varieties *(Stützsorten)*, having the same reaction pattern as the differentials,
2. additional differentials *(Zusatzsorten)*, for the differentiation of sub-races,
3. screening varieties *(Suchsorten)*, which have always been resistant and therefore may serve to detect new races.

Results are presented in table A.23.5.

Peko is a good supporting variety to Heines Kolben. Halle 3435/46 and Vilmorin 27 might prove to be supporting varieties to Chinese 166 and Vilmorin 23 respectively. Alba, Blé des Dômes, Merlin and Carpo might become additional differentials, when further testing confirms the first impression. Bonus, Felix, Funo, Heines 110, Hope × Timstein, Minister, Panter, Reichersberg 42, Riebesel 51-52 and Selkirk seem to be promising screening varieties.

Admittedly the tests were not very extensive. Final conclusions cannot be drawn before the varieties have been tested during another season, using more different isolates.

23.6 The races, differentiated in the greenhouse

Difficulties arise in comparing Braunschweig, Cambridge (MANNERS, 1950; BATTS, 1957a) and Wageningen data. These difficulties find their origin in divergent opinions regarding the discriminative ability of the differentials. In Braunschweig, Heines Kolben and Chinese 166 are good differentials, Vilmorin 23 and Carstens V are nearly useless, though a good line of Vilmorin 23 has been found recently. Webster is regarded as an indispensable differential, though the relative poverty of its discriminative ability is recognized. Of the other differentials only Spaldings prolific is worthy of consideration, as it differentiates between two races with the differences i–0 and 0–4, differences claimed to be reproducable.

In Wageningen, Vilmorin 23, Heines Kolben, Carstens V and Chinese 166 are good differentials. The other differentials are at this time too poor to be considered seriously. The fact that Carstens V was satisfactory and Webster was useless completely upset the scheme presented by FUCHS (1960), reproduced in table 23.1. Therefore it was necessary to make a temporary race classification to be used until the time comes when the differences between the Braunschweig and Wageningen data will be cleared up.

The temporary Wageningen classification of yellow rust races is based on four good differentials, which show usually major differences under Wageningen conditions. The Wageningen key allows for 16 races, of which 7 have been found

Table 23.6.a Temporary Wageningen key for race identification in the greenhouse

differentials / races	Vilmorin 23-W 6	Heines Kolben-W 7	Carstens V-W 8	Chinese 166-W 10
W 1	+	+	+	+
W 2	+	+	+	—
W 3	+	+	—	+
W 4	+	+	—	—
W 5	+	—	+	+
W 6	+	—	+	—
W 7	+	—	—	+
W 8	+	—	—	—
W 9	—	+	+	+
W 10	—	+	+	—
W 11	—	+	—	+
W 12	—	+	—	—
W 13	—	—	+	+
W 14	—	—	+	—
W 15	—	—	—	+
W 16	—	—	—	—

— = resistant
+ = susceptible

(tables 23.6.a, A.23.6.a and A.23.6.b). In some cases the relation between the Braunschweig, Cambridge and Wageningen races could be established, since type isolates have been exchanged between the stations (table 23.6.b). In other cases the relation between the Wageningen, Cambridge and Braunschweig races have not yet been established.

Race W4: This race is only known from one isolate, the Braunschweig type isolate for race 1x.

Race W 6: This race is known from two isolates. The reaction spectrum is like that of the Braunschweig races B 2x and B 55, but the Braunschweig type isolates of these two races are not compatible with Carstens V in Wageningen.

Race W 8: The infection spectrum of race W 8 is given by the Braunschweig type isolates of the races B 2x and B 55. The difference between these two

Table 23.6.b Relation between some Wageningen (W), Braunschweig (B) and Cambridge (C) races according to seedling tests carried out in Wageningen and Braunschweig

W 4	=	B 1x		
W 6	=	B .		
W 8	=	B 2x/55	=	C 2b
W 12	=	B 54		
W 13	=	B 27/53		
W 14	=	B 6/7/7xV_1		
W 16	=	B .		
		B 7x	=	C 8b

races is doubtful for two reasons: the formalistic reason being that the difference made is not a major difference 0 versus 4 but a minor difference i–0 versus 0–4, the epidemiologic reason being that no field observations support the hypothesis of the existence of these two races as distinct entities.

Race W 12 must be identical with race B 54, as these races are in both keys the only races with compatibility to Heines Kolben and incompatibility to Vilmorin 23.

Race W 13 is identical with race B 27/53 in view of its compatibility to Chinese 166.

Race W 14 shows the same reaction spectrum as the Braunschweig races B 17/26 and B $7xV_1$, which in Braunschweig, but not in Wageningen, can be differentiated on Webster.

Race W 16 cannot be identified with any of the Braunschweig races at the present time. It will be proved later that race W 16 is a complex of widely diverging races, which cannot be separated by greenhouse seedling tests (24.42).

23.7 Frequency distributions of races over varieties and over countries

From the data of Fuchs (1960) the relative frequencies of some races have been computed for a few North-west European countries (table 23.7.a). The race spectra of the different countries are rather similar, though the Netherlands have a high percentage of race W 12 and Switzerland is lacking races of the B 7x group. For most countries the number of observations is too low to be able to draw reliable conclusions. The conservative conclusion is that the races in the North-west European countries are as yet represented in an approximately constant frequency in the samples, coming from the International Yellow Rust Trials. Aberrations from this rule are present, but cannot be interpreted without supplementary information. In another context, Oort (1955) studied the distribution of the older physiologic races of yellow rust in Europe.

The frequency distribution of races over the original host varieties, from which they have been isolated (table 23.7.b), is more or less independent of the original host variety, though on Michigan Amber and still more on Cappelle a

Table 23.7.a Braunschweig greenhouse tests: frequency distributions of races over countries, 1956–1958. Data derived from Fuchs (1960).

races / countries	frequencies					number of isolates tested
	W .	W 8	W 12	W 13	W 14	
	B7, 7x, 7A, 7/8, 5/6	B 2x/55	B 54	B 27/53	B $7xV_1$, 17/26	
Belgium	.8	.1	.0	.0	.1	13
Denmark	.8	.0	.0	.1	.0	26
France	.5	.2	.1	.2	.0	23
Germany	.7	.1	.1	.0	.0	141
Great Britain	.7	.0	.1	.1	.1	43
Netherlands	.5	.1	.3	.1	.1	98
Sweden	.7	.0	.1	.1	.1	9
Switzerland	.0	.4	.3	.2	.0	9
total	.6	.1	.1	.1	.1	362

.0 = frequency between 0 and .05

TABLE 23.7.b Braunschweig greenhouse tests: frequency distributions of races over varieties, 1956–1958. Data derived from FUCHS (1960).

varieties \ races	frequencies					number of isolates tested
	W .	W 8	W 12	W 13	W 14	
	B7, 7x, 7A, 7/8, 5/6	B2x/55	B 54	B 27/53	$B7xV_1$, 17/26	
Michigan Amber	.4	.4	.1	.1	.0	28
Harvest Queen	.7	.1	.0	.1	.1	26
Persian	.8	.0	.2	.0	.0	23
Rubis	.7	.0	.1	.1	.1	29
Heines VII	.7	.1	.1	.0	.0	82
Cappelle	.1	.5	.1	.3	.0	11
total	.6	.1	.1	.1	.0	468

.0 = frequency between 0 and .05

high percentage of race W 8 has been found. The conservative conclusion is that most races are so versatile that they can be found on any host variety, even if other data show these hosts to be differential varieties. The foregoing does, however, not mean that all races can cause an epidemic on any host variety.

These conclusions are not very helpful, generalizations as they are. A breeder likes to know which races do damage, where and on what variety. Such concrete information cannot be given by greenhouse work, nor can the greenhouse work explain the curious epidemics of the last few years. Too much time has been wasted in greenhouse problems, interesting in themselves, but of little importance for practical agriculture; field work is needed to answer the questions of breeder and epidemiologist.

24 PHYSIOLOGIC SPECIALIZATION IN THE FIELD

24.1 The problem and some techniques to solve it

Though we are accustomed to the use of seedling plants for race differentiation, there is no serious objection to the employment of mature plants. Indeed, this is the only way when the parasites can only be recognized in the adult stage, e.g. smut and bunt. The problem to be dealt with in the following pages, is the behaviour of the rust races in the field in the mature plant stage.

Several techniques present themselves. Plants can be grown from seedling to mature plant in the greenhouse or in conditioned climate chambers. Lack of room and doubt as to the value of results obtained under these unnatural growing conditions rules out this possibility.

DOLING grew his varieties in pots in the open and brought them into the greenhouse in the shooting stage to be tested. MANNERS (1950) inoculated isolated plots, containing different varieties in 3 repetitions, with spore suspensions of different races. He obtained useful results, but the level of infection reached was insufficient for the present purpose. KÜDERLING (1937) and MESDAG (1958) used race nurseries and obtained useful results.

Two techniques have been chosen: one was the technique of race nurseries, described in 14.6, the other technique made use of the data, collected by the

International Yellow Rust Trials (15). The main difference between the two techniques is that in the latter trials spontaneous infection is awaited for, while in the race nurseries artificial infection is applied.

24.2 Data processing

24.21 The choice of the basic parameter, DA

The data provided by the race nurseries and the International Yellow Rust Trials cannot be easily compared without undergoing transformation. The computational procedure is the same for both sources of data; it will be described in the following pages.

The observations of a yellow rust trial or race nursery consist for each variety of a growth stage GS, an infection type IT and a degree of attack DA. The complete series of observations from one trial on one particular day has been called an "observation set".

IT is a parameter running from 0 to 4, with only five grades. In the field it is ill defined, variable according to weather conditions and difficult to assess for the untrained observer and even for his trained colleague. Though IT is a good parameter of susceptibility in the early stages of infection, often the only parameter available, in the later stages of infection it is frequently obscured by secondary effects.

DA as a parameter is more detailed than IT, as it runs from 0 to 10 with eleven grades. In contrast to IT, which is essentially a qualitative characteristic, DA is a quantitative characteristic based on the percentage of leaf surface affected. When necessary it can be measured with the help of a planimeter. In view of these arguments DA has been chosen as the basic parameter.

24.22 The selection of observation sets

Not all data from the race nurseries and the International Yellow Rust Trials can be used for the study of race specialization. A large number of observation sets has to be rejected for one or more reasons, according to certain criteria discussed below.

The main object of this section being the mature plant, the question arises: at which GS is a wheat variety mature with regard to its response to yellow rust infection? The varieties Carstens VI and Flamingo show a marked transition in the response to the Heines VII race, both being susceptible in the seedling stage and resistant in the adult stage. Careful observations in the field and in comparative trials showed that the transition occurred somewhere between GS 5 and 8. In one year Carstens VI may attain resistance first, in another year Flamingo. Normally, both varieties have attained their maximal resistance in GS 8. Although other varieties may behave somewhat differently, the observations justify the following criterium: all observations sets with a median growth stage under 9 should be rejected. Sometimes it may be necessary to test the winter wheat and the spring wheat series separately against this criterium.

In the foregoing remarks it is taken for granted that the rust inoculum is regularly distributed over the whole trial. This is approximately true during a severe epidemic, either natural or artificial, but in the International Yellow Rust Trials the attack is generally of the focal type. The use of susceptible varieties at regular distances throughout the trials with the purpose of trapping, multiplying and dispersing the inoculum counterbalances the effect of focal infection to

TABLE 24.23 Table for the transformation of DA into RDA

DA \ IL	6	7	8	9	10
0	0	0	0	0	0
1	1.7	1.4	1.2	1.1	1.0
2	3.3	2.9	2.5	2.2	2.0
3	5.0	4.3	3.7	3.3	3.0
4	6.7	5.7	5.0	4.4	4.0
5	8.3	7.1	6.2	5.6	5.0
6	10.0	8.6	7.5	6.7	6.0
7	.	10.0	8.7	7.8	7.0
8	.	.	10.0	8.9	8.0
9	.	.	.	10.0	9.0
10	.	.	.	.	10.0

entries: relative degree of attack RDA

some extent. Careful observation of many trials showed the balance to be approximately equal at an infection level 6. The infection level IL is a characteristic of the observation set; it is defined as the highest DA observed in an observation set.

Another assumption is that the varieties will show their inherent propensities of susceptibility and resistance at any infection level. At the lower levels of infection, however, susceptibility is often underestimated, because a susceptible variety may temporarily escape the infection. At the highest levels of infection resistance will be underestimated, because moderately resistant varieties may show a high DA, due to repeated infection by inoculum from their more susceptible companions. The former underestimation is the worse, and it was decided that from an IL 6 upward the susceptibility of the varieties could be fairly well judged. So the second rejection criterium is: all observation sets with an infection level under 6 should be rejected.

A final reason for rejection of observation sets is found in the different ripening rates of the varieties within a trial. Observation sets with median GS 11.1, 11.2 and 11.3 are critically considered. When, compared to earlier observation sets of the same trial, they show a marked drop in their IL due to ripening, or marked discrepancies due to differences in precocity, such observation sets are rejected.

TABLE 24.24 Table for the transformation of RDA into RDAP

RDA units \ decimals	0	1	2	3	4	5	6	7	8	9
0	0	0	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0	0	0
3	0	0	0	0	0	0	0	1	1	1
4	1	1	2	2	2	3	3	3	4	4
5	5	5	6	6	7	7	8	8	9	9
6	10	11	12	13	15	16	17	19	21	23
7	25	27	29	32	34	37	39	42	45	47
8	50	52	55	57	60	63	65	68	70	73
9	75	78	80	83	85	88	90	93	95	98
10	100	.	.	.	.	.	.	.	.	.

entries: relative degree of attack percentage RDAP

Notwithstanding these rejection criteria the number of observation sets accepted is considerable.

24.23 The relative degree of attack, RDA

The basic parameter chosen is the DA. It is, however, not an ideal working parameter. One reason is that it is not easily visualized, as is the case of percentage values. The second reason is that it does not take into account the general infection level IL, so that it is difficult to compare observation sets at different infection levels. The solution of this problem is a transformation of the basic parameter into a working parameter using a well defined key.

Each DA can be expressed as a relative value, the relative degree of attack RDA, in the following way: $RDA = \frac{10.DA}{IL}$. The computational work was simplified by the use of table 24.23.

24.24 The relative degree of attack percentage, RDAP

When more observation sets are available for one trial, the data of each variety can be averaged. But which data and which average? Comparison of several data and averages showed that the arithmetical average of RDA values

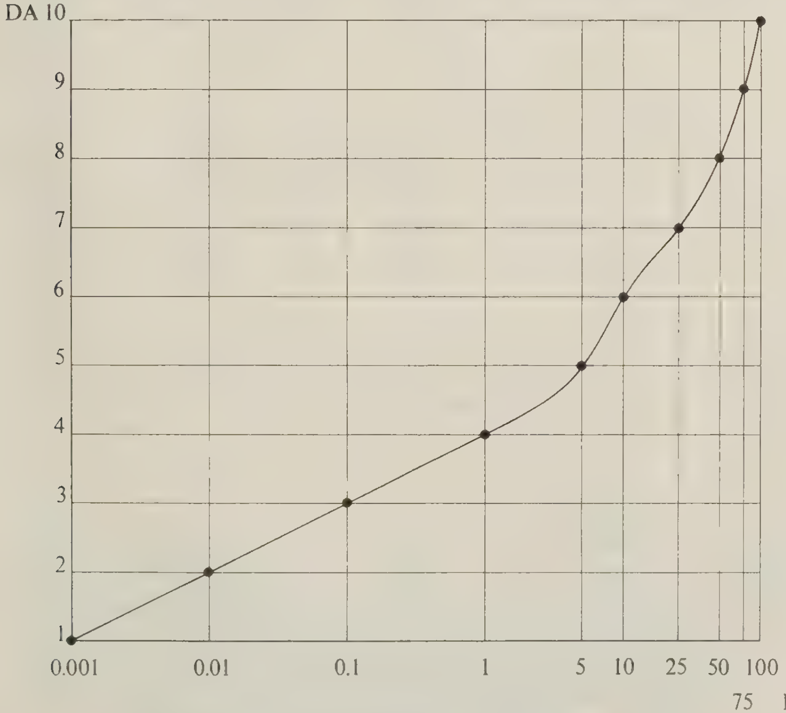


FIG. 24.24 The relation of the degree of attack DA to the percentage of attack PA. PA is plotted on a logarithmic scale, DA on a linear scale.

tended to overestimate the lower observations to an undesirable degree. When RDA values were transformed into percentage values before averaging, this overestimation of lower values did not occur.

For the transformation of RDA into relative degree of attack percentage RDAP another transformation table was used (table 24.24). The values of this transformation table were found by graphical interpolation in the graph of fig. 24.24, representing the relation between DA en PA (percentage of attack).

RDAP is our working parameter. It is the percentage of attack after transformation of the data from the observed IL to IL = 10, using a specified non-linear transformation.

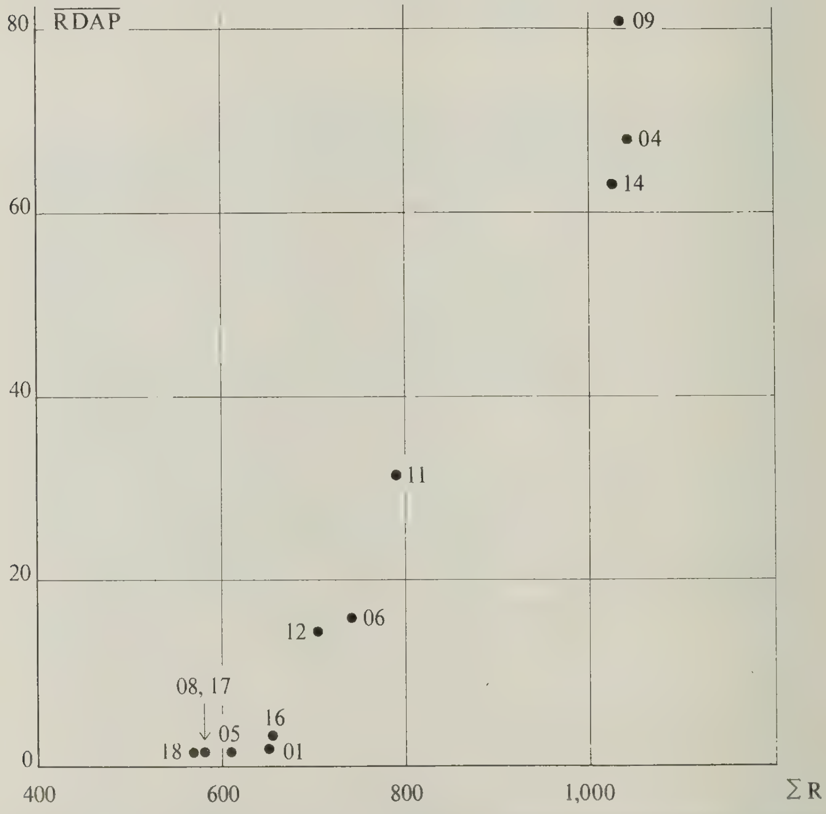


FIG. 24.26.a The relation between two independent parameters of susceptibility: ΣR, the "parameter of earliness", and $\overline{RDAP}$. Data from the International Yellow Rust Trials, 1958, restricted trials. Each dot represents the average of c. 110 trials, scattered all over North-west Europe. The numbers with the dots refer to the varieties of table A.24.42.

ΣR = sum of the rank number per variety = parameter of earliness

$\overline{RDAP}$ = average RDAP per variety over all trials

24.25 The average infection spectrum, AIS

An observation set consists of DA values. After transformation from DA into RDAP the set of transformed observations is called a "relative infection spectrum", RIS. RIS characterizes a rust population present at a specified locality and date.

When more RIS.s from one trial are available the RDAP.s of each variety can be averaged, giving an average relative degree of attack percentage, ARDAP. The resulting spectrum of ARDAP.s has been called the "average infection spectrum", AIS. An AIS characterizes the rust population at a given locality, incorporating observations of different observation times, growth stages, infection levels and sometimes even observers. The advantage of a characteristic

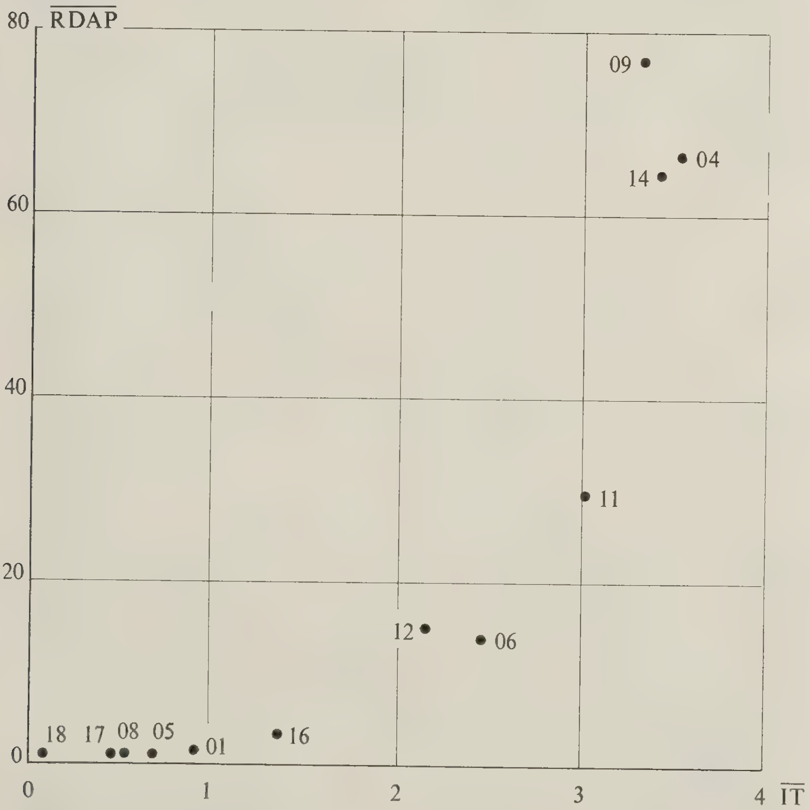


FIG. 24.26.b The relation between two independent parameters of susceptibility: $\overline{\text{IT}}$ and $\overline{\text{RDAP}}$. Data from the International Yellow Rust Trials, 1958, restricted trials. Each dot represents the average of c. 110 trials, scattered all over North-west Europe. The numbers with the dots refer to the varieties of table A.24.42.

$\overline{\text{IT}}$ = average IT per variety over all trials

$\overline{\text{RDAP}}$ = average RDAP per variety over all trials

incorporating all observations available is considerable, such a characteristic being a fair reflection of the varietal responses to the race or races present at a specified locality with specified environmental conditions.

24.26 A comparison between some parameters of susceptibility

The Preliminary Reports on the International Yellow Rust Trials contained tables in which the highest DA observed per variety and per trial was used as a parameter of susceptibility. As has been explained, this parameter is dependent on the IL and it has therefore little comparative value.

Another parameter of susceptibility can be constructed, using the time of the first observation of yellow rust on the varieties of a trial. For each trial the varieties can be assigned rank numbers according to the order in which they have been found to be infected. For each variety the sum of the rank numbers ΣR from a large number of trials serves as a parameter of "earliness of infection" and, in consequence, of susceptibility. For each variety ΣR can be compared to the average of the corresponding RDAP values, $\overline{RDAP}$ (not to be

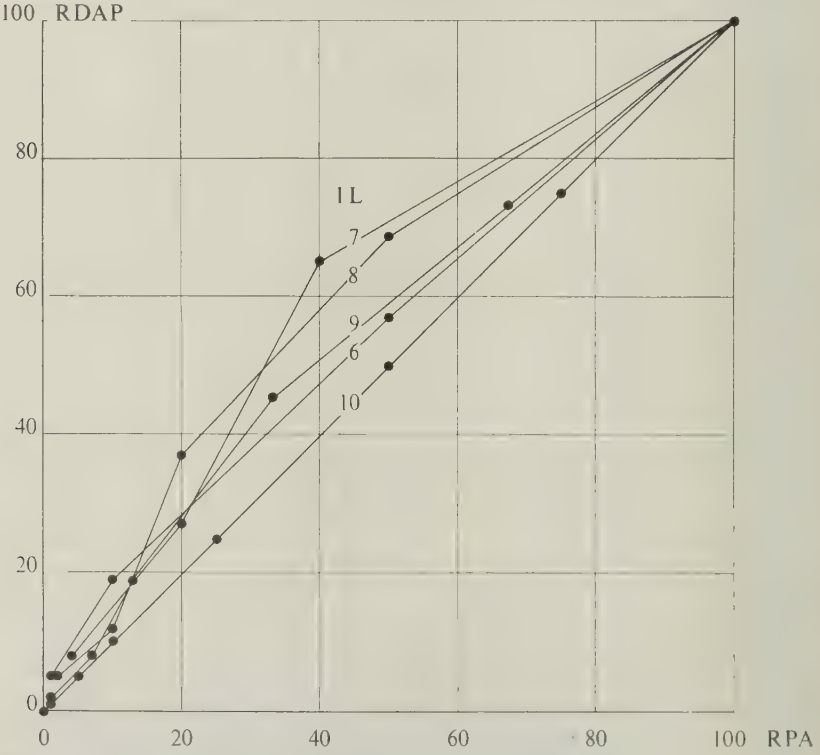


FIG. 24.26.c Relation between RPA and RDAP at different IL.s.
RDAP = relative degree of attack percentage
RPA = relative percentage of attack
IL = infection level

TABLE 24.26 Table for the direct transformation of DA into RDAP

DA \ IL	6	7	8	9	10
0	0	0	0	0	0
1	0	0	0	0	0
2	0	0	0	0	0
3	5	2	1	0	0
4	19	8	5	2	1
5	57	27	12	8	5
6	100	65	37	19	10
7	.	100	69	45	25
8	.	.	100	73	50
9	.	.	.	100	75
10	.	.	.	.	100

entries: relative degree of attack percentages RDAP

confused with ARDAP!), computed for the same trials. This has been done for the restricted trials of the 1958 International Yellow Rust Trials fig. 24.26.a). The relation between ΣR and $\overline{\text{RDAP}}$ is monotonous, which implies that both values are estimates of the same susceptibility. RDAP, however, is a more reliable parameter than R.

The relation between IT and RDAP is demonstrated by fig. 24.26.b. For every variety of the restricted trials of the 1958 International Yellow Rust Nurseries the average value of IT, $\overline{\text{IT}}$, and of RDAP, $\overline{\text{RDAP}}$, are given. The relation between $\overline{\text{IT}}$ and $\overline{\text{RDAP}}$ is monotonous; both values are estimates of the same susceptibility. RDAP is the more versatile estimate of the two.

Though RDAP is a good parameter of susceptibility it is based on DA values, defined by the International Scale for the observation of the International Yellow Rust Trials. The percentage of attack, PA, is a more generally used unit of disease assessment. PA can be transformed into a relative percentage of attack, RPA. In fig. 24.26.c the RDAP and the corresponding RPA values have been compared at different IL.s. With lower IL.s and intermediate DA.s the RDAP tends to overestimate the infection as compared to RPA. A study of several possible transformations, including logarithmic and angular transformations, convinced the writer that this kind of overestimation was just what was needed to improve the reproducibility of RISpectra, observed at different IL.s. When several successive RIS.a from one trial are averaged to an AIS the effect of the mentioned overestimation is minimized. There is no objection to comparing AIS.a computed with RDAP to those computed with RPA, but some differences remain. For the transformation of DA into RPA see table A.24.26.

The RDAP transformation has been described as a two-step transformation, using tables 24.23 and 24.24. It can be made a one-step transformation using table 24.26, which is a combination of the tables 24.23 and 24.24.

24.3 Variation in field data

24.31 Variation in assessment between observers

Though the instructions for the observers are terse, they nevertheless leave some room for personal interpretation. As there were about 150 International Yellow Rust Trials, there were nearly as many observers and interpretations.

In the course of the years, the writer visited most of the trials to discuss the technique of assessment with the local observers; these visits promoted a great advance towards uniform assessment.

There still remain, to some extent, differences between observers. Part of these differences are differences in the level of assessment. One observer may give all varieties one DA point more than another observer. Such differences in the level of assessment are counteracted by the transformation of DA into RDAP values.

A more frequent difference in assessment is that of underestimation and overestimation as compared to the writer's assessment, which was the standard employed. It was noticeable that where the experience of the observer was limited, the overestimation of the higher DA.s and the underestimation of the lower DA.s were greater.

Table A.24.31 represents an example of two observation sets from trial 3360 on July 10th, 1958, one by the local observer and one by the writer. The coincidence in the day of observation was accidental, each observer being ignorant of his colleague's visit. In the first two columns the original notes (DA) are compared. In the third column underestimation (u) and overestimation (o) by the local observer have been indicated, taking into account only differences of more than 1 DA point. Underestimation occurs more frequently. In the next two columns the resulting RDAP.s are compared.

As a result of the transformation the underestimation is no longer apparent. The susceptible varieties Harvest Queen, Rubis and Persian are severely infected in both infection spectra, Heines VII is intermediate, Redman is low, the remaining varieties are practically not infected. The tendency of both RIS.a is the same, although the actual values differ.

24.32 Variation between successive RIS.a from one trial

The rust may come early or late, it may come as a general infection or start as a focus in the trial, it may develop into a severe epidemic or stop in the initial stage. To overcome such variables, only those data should be selected which give an impression of the average behaviour of the varieties during an epidemic.

Table A.24.32 presents the original data and their RDAP from International Yellow Rust Trial 3510 at Wieringerwerf, 1957. The infection started early, with a focus on Ø tofte 56, which in the adult stage has only a moderate susceptibility. About the beginning of May the focal effect is no longer apparent, the IL is then 7 or 8, the GS = 8. The mature plant resistance is at that time not yet fully developed, as can be seen in the observations on Michigan Amber (in 1957 a line was used with relatively high mature plant resistance) and Ø tofte 56. When the observational data are within the admission limits 3 observation sets are available, of which the last has to be rejected because of irregularities due to ripening (e.g. Plantahof III).

Two observation sets, very similar, remain and their RDAP.s have been averaged into ARDAP.s, which give a good picture of the rust population present at trial 3510 in 1957.

This example represents the general situation. The elimination criteria are fixed in such a way that only 1 to 4 observation sets per trial remain, which have shown good similarity with each other and which give an AIS, representative for the local rust population.

24.33 Spontaneous infection: variation between trials, subjected to identical conditions of infection

In 1960, sixty race nurseries were established in a 30 ha. field of winter swede rape, at a minimum distance of 900 m. from the nearest commercial wheat fields, about 500 ha. of the winter wheat Triumph. In many nurseries the inoculation failed. All of the nurseries, however, were subjected to spontaneous infection from the large Triumph field, where a severe epidemic of yellow rust developed.

The infection was late; it had the character of a spore cloud, blown in by westerly winds and causing a fairly regular infection. When the infection had advanced sufficiently, notes were taken (28–6 and/or 6–7).

28 AIS.a, each based on 1 or 2 observation sets, could be related with certainty to the spontaneous infection; they are represented in table A.24.33. The varieties can be divided into 3 groups:

1. highly susceptible varieties, Michigan Amber, Harvest Queen and Persian,
2. resistant varieties, the largest group,
3. varieties with intermediate susceptibility, among which were Triumph itself, Probus and others.

The great range of the ARDAP.s in the last group is remarkable, Probus varying from 2 to 75, Triumph varying from 8 to 75. The IL.s varied from 7 to 10 with median value 9.

This material is unique as 28 trials are subjected to the same infection under identical climatic conditions. The great variation in the results of the intermediate group are disappointing. They can be attributed only in part to relatively small differences in soil type and relatively large differences in the physical development of the trials. Varieties of the intermediate group tend to show low ARDAP.s, when the physical development of the trial as a whole and of the varieties in particular is subnormal.

As a conclusion it can be stated that a yellow rust trial under conditions of late spontaneous infection may give variable results, especially in the group of varieties with intermediate susceptibility, but that as a rule the main characteristics of the rust population will come out clearly. In the present case these characteristics are compatibility with some commercial varieties as Probus and Triumph, and incompatibility with other commercial varieties as Heines VII, Alba and Etoile de Choisy.

24.34 Spontaneous infection: variation between localities

In 1959 yellow rust was widely spread in Switzerland. A comparison of the AIS.a of five different International Yellow Rust Trials, scattered all over the country, shows a reasonable agreement, see table A.24.34. It must be noted that notwithstanding the RDAP transformation minor differences in infection intensity remain. This is clearly demonstrated in table A.24.34, where the values of trial 8410 are much lower than those of the other trials. The main characteristics of the rust population are clear in at least four of the five trials. These characteristics are incompatibility with Rubis and Little Club and a number of Dutch commercial varieties and compatibility with Probus.

24.35 Spontaneous infection: variation between years

The International Yellow Rust Trial Emmeloord 3520 gives a good example of an identical attack developing in two successive years, 1958 and 1959 (table A.24.35). The continuitv of the rust population had been ascertained by summer, autumn and winter observations. The two localized epidemics developed the same characteristics: compatibility of the rust population with Rubis, Heines VII, Flamingo, Heines IV and Peko, incompatibility with Alba and Etoile de Choisy. Again the variation is greater in the intermediate group of varieties (Flamingo, Peko) than in either the susceptible or the resistant groups.

Several other examples of good reproducibility of AIS.a from different years could be given.

24.36 Artificial infection: variation between isolates and race nurseries

Theoretically, variation between AIS.a should be small in race nurseries under conditions of severe artificial epidemics. In practice, this is not always the case. Much depends on the general vigour of the plants to be tested, on the type of spreader, whether universally susceptible or differential, on the time of inoculation and on the weather conditions during the beginning of the artificial epidemic. Differential spreaders are less susceptible than universal spreaders, but they give good results under favourable conditions; under the adverse conditions of 1960, however, the results with differential spreaders were not satisfactory.

Table A.24.42.f. represents AIS.a from different isolates, years of testing and soil types. The results are neither better nor worse than those obtained with other isolates. The general tendency is always the same: highly susceptible varieties and resistant varieties can be recognized in any AIS. The group of varieties with intermediate susceptibility, among which are the important commercial varieties, shows great variability. Major differences such as Heines VII and Peko – susceptible, Cappelle and Nord – resistant, come out clearly.

24.37 Variations between infections, artificial and spontaneous

Artificial and spontaneous infections can give different results, mainly because artificial infection generally gives a severe epidemic, whilst spontaneous infection often only leads to a mild epidemic.

Table A.24.37 gives an idea of the effect of the two types of infection. Column A is composed of the $\overline{\text{ARDAP}}$ of two race nurseries in Oostelijk Flevoland, 1960, with successful artificial infection at an early date. Readings have been stopped when the spontaneous infection gained in force. Column S is composed of the $\overline{\text{ARDAP}}$ from the 28 spontaneously infected race nurseries in Oostelijk Flevoland, 1960 (table A.24.33). The difference between the two sets of data, as usual, is in the group of varieties with intermediate susceptibility, which were infected to higher DA.s under the more severe conditions of artificial infection, see Probus, Triumph and Heines IV. The order of the varieties, ranked in decreasing $\overline{\text{ARDAP}}$, is not dependent on the type of infection.

24.38 Statistical aspects of variation

The data from International Yellow Rust Trials and race nurseries do not lend themselves easily to a statistical analysis. The reasons can be understood

best when considering table A.24.33. Resistant varieties show a skew distribution of ARDAP.s with a top at 0, susceptible varieties show a skew distribution with a top at or near 100. The intermediate group, among which is Triumph, shows a flat distribution with a large range. The picture remains the same whether DA, PA or any transformation of these values is studied. Generally speaking, transformation increases the deviation from the normal distribution of these values. An analysis of variance is impossible because of the absence of normality in the frequency distribution of the original data.

Better results might be obtained with ranking methods. Ranking methods have not yet been tried, mainly because a rank number cannot be vizualized so easily as a percentage value.

24.4 The races

24.41 Race and population characteristics, RC and PC

An AIS is characteristic for the local rust population (24.25). When this local rust population descends from a unipustular culture as in the race nurseries, the resulting AIS is characteristic for the race used. When more AIS.a, representing one race, are available, they must be combined into a final characteristic, the "race characteristic" RC.

The computational procedure used is the following:

1. the number of observation sets, from which an AIS is computed, is called n,
2. for each variety the product n.ARDAP is computed,
3. for each variety the products n.ARDAP are summarized over all trials to the sum Σ (n.ARDAP),
4. the sum Σ (n.ARDAP) is divided by the sum of the numbers of observation sets over all trials Σ n,
5. the resulting quotient is called "compatibility index":

$$\frac{\Sigma\,(\text{n.ARDAP})}{\Sigma\,\text{n}} = \text{CI}$$

The CI.s of a set of varieties, infected with the same race, form together a "race characteristic", RC. The CI.s of a set of races, inoculated to one variety, form an inventory of the genes for resistance of that variety.

The judgment of a trained biologist is necessary to determine the right combinations of AIS.a, as no two AIS.a are identical. Not only the actual value of the ARDAP.s should be taken into consideration, but also the rank of the varieties, when ranked from high to low ARDAP. When spontaneously infected trials are studied, the rank of a variety is even more significant than the value of its ARDAP. The biological judgment is the same in field and in greenhouse experiments, though the experimental techniques are different. In the greenhouse two isolates from one race will seldom give identical reactions; nevertheless they are judged to belong to the same race after due consideration of such subtleties as incubation time or the influence of light intensity. Comparable subtleties come into the interpretation of field data in the form of considerations on the influence of drought or infection pressure.

A RC can be assigned a weight, indicating the number of observations on which it is based. This weight is composed of three numbers, the first indicating the number of years, the second the number of trials and the third the number of observation sets involved in the RC. A weight 2.3.6 means that the RC is

based on six observation sets from three trials in two different years. This weight does not imply that for each variety there are six observations, because the varietal composition of the trials is slightly changed each year.

Every year adds new data to the CI.s, the RC and its weight. The fluctuations in the CI.s, computed anew every year, will become smaller with an increasing number of observations and eventually the CI.s will attain a stable final value.

RC.s, based on race nurseries, can be used to interprete AIS.a due to spontaneous infection. When the spontaneous infection of a trial is caused by one race only, the observations of that trial can be incorporated into the RC, see for example the RC of the Triumph race, table A.24.42.j.

When the infection of a trial is due to two races, one known and one unknown, something about the unknown race can be learned by a subtraction procedure. Varieties without infection are resistant to both races. The data from varieties, susceptible to the known race, must be discarded because they might also have been due to the unknown race. Data from varieties, resistant to the known race but infected in the trial, can be confidently ascribed to the unknown race. Cases of marginal infection must be left to the biologist's judgment. An example of the subtraction procedure, resulting in an incomplete RC, is given by table A.24.42.i, representing the computation of the partial RC of the Cappelle race.

"Population characteristics" (PC.s) for specified geographic areas can be computed from data of the International Yellow Rust Trials Project in the same way as RC.s have been computed from data of race nurseries.

The method described results in the identification of a number of "field races", based entirely on the reactions of the mature plants. These field races are usually named after their carrier variety, e.g. Heines VII race. Populations have been given geographic names, e.g. Grecian population.

24.42 Field races and populations

Table 24.42 gives the CI.s of some field races and field differentials (full data in tables A.24.42.a–t). A Rubis and a non-Rubis group can be recognized; within the Rubis group there is a Heines VII group. Little Club acts as a supporting differential to Rubis; Merlin supports Heines VII.

Race $7xV_1$ (race B $7xV_1$, W 14; table A.24.42.a)

This race does not infect any commercial variety tested.

Isolate 115, a Braunschweig monospore isolate of race B $7xV_1$ kindly furnished by Dr. Eva Fuchs, has been tested in one 1960 race nursery.

Fuchs (1960) isolated race B $7xV_1$ for the first time from a Dutch sample, collected in June, 1956. The race has been isolated repeatedly from several commercial varieties. No explanation can be offered for the discrepancies between Fuchs' and the writer's findings.

Heines VII race (race W 16; table A.24.42.b)

This race, belonging to the Rubis group, is compatible with Heines VII and Merlin, but not with the other differentials.

Two unipustular isolates from Heines VII 1958, isolates 8589 and 8600, have been tested in race nurseries. The Heines VII race appeared on International Yellow Rust Trials in Belgium, England and the Netherlands.

In the Wageningen greenhouse the race cannot be distinguished from the

Alba and Triumph races, all reacting as race W 16; it is probably identical with a race of the Braunschweig 7x group.

Leda isolates (race W 16; table A.24.42.c)

The Leda-isolates belong to the Rubis group. They are virulent to Heines VII and Merlin, but less virulent to Leda, Heines IV, Flamingo and Alba.

The two Leda isolates tested, 9791*a* and 9791*b*, come from the same field in Het Bildt 1959.

The greenhouse reaction of isolate 9791*b* is between those of races W 12 and W 16, as in several repetitions Heines Kolben reacted with type 2 ⊏ and Peko with type i–4. This is the only example of Heines Kolben and Peko not being discriminative differentials. On the basis of mature plant reactions, especially that of Heines Kolben, the isolates have been provisionally grouped into race W 16, next to the Heines VII race.

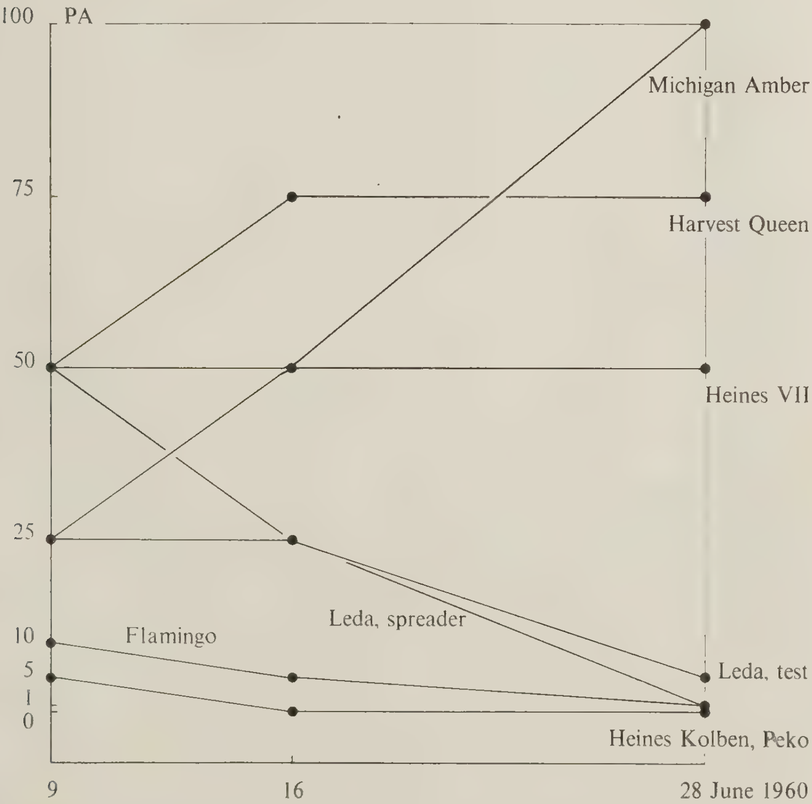


FIG. 24.42 Observations from race nursery 0012, inoculated with an unipustular isolate from Leda/Het Bildt/9791*b*. On some varieties the percentage of attack PA increases in the course of time; on others, Leda included, PA decreases as the mature plant resistance comes to expression.

TABLE 24.42 The field races and populations. Entries are compatibility indexes CI.

Field key	Race 7xV$_1$	Heines VII race	Leda isolates	Heines VII-Heines IV race	Flamingo race	Peko race	Heines Kolben race	Chinese race	Cappelle race	Triumph race
Braunschweig key	B 7xV$_1$	.	.	B 7x	B 54	B 54	B 1x	B27/53	B 2x	.
Wageningen key	W 14	W 16	W 16	.	W 12	W 12	W 4	W 13	W 8	W 16
1 Carstens V	0	0	0	0	0	0	0	16	0	1
2 Chinese 166	2	2	0	.	0	0	0	92	.	0
4 Rubis	73	93	77	.	94	90	100	2	.	0
7 Staring	0	0	0	1	0	0	0	0	24	0
8 Nord	0	0	0	1	0	0	1	0	66	0
9 Cappelle	0	0	0	0	0	0	0	0	20	0
10 Triumph	.	2	.	.	0	0	0	1		47
11 Heines VII	0	41	38	82	39	50	0	0	.	0
13 Merlin	0	31	26	.	46	41	0	0	.	0
17 Leda	0	0	21	.	0	0	0	0	.	0
18 Alba	0	1	8	.	0	1	3	0	.	0
22 Etoile de Choisy	0	0	2	0	0	0	0	1	0	0
23 Marne	0	0	0	0	1	0	0	0	0	0
24 Carest	0	0	0	.	0	0	0	0	.	0
28 Heines IV	.	2	18	41	37	0	0	0	.	9
29 Flamingo	1	1	10	.	24	2	0	0	.	0
31 Peko	0	0	3	1	10	37	8	0	1	0
32 Heines Kolben	0	0	4	.	53	47	77	0	.	0
34 Little Club	22	54	66	.	63	68	79	1	.	2
35 Hope × Timstein	.	.	.	.	3	0	.	.	.	0
36 Selkirk	0	.	0	0	0	0	.	2	0	0
weight	1.1.2	1.2.5	1.3.6	1.3.5.	3.5.16	3.5.11	1.4.11	2.4.10	2.3.9	1.30.58

. = no data available.

Alba race	Etoile de Choisy race	Heines IV race	Probus race	Race 2x/55	Race 7x	Grecian population	Iberian population	Levantine population	Kenya population	Field key
.	.	B 7x	.	B 2x/55	B 7x	.	.	.	.	Braunschweig key
W 16	W 8	.	.	W 8	.	.	.	.	.	Wageningen key
0	1	0	0	0	0	.	0	0	.	Carstens V 1
0	0	.	0	0	0	.	0	0	.	Chinese 166 2
0	1	4	0	0	0	58	65	1	.	Rubis 4
0	1	0	1	0	0	2	10	0	.	Staring 7
0	14	0	0	3	0	1	17	0	.	Nord 8
0	0	0	0	2	1	2	7	0	.	Cappelle 9
0	.	0	0	0	12	2	7	0	.	Triumph 10
0	0	0	0	0	0	0	8	0	.	Heines VII 11
0	0	0	0	0	0	.	17	0	.	Merlin 13
0	0	0	0	0	0	1	0	0	.	Leda 17
46	0	0	0	10	0	2	1	0	.	Alba 18
0	5	0	1	0	0	3	6	0	.	Etoile de Choisy 22
0	6	.	0	0	0	1	0	0	.	Marne 23
0	6	.	0	1	0	.	0	0	.	Carest 24
0	.	75	0	0	2	.	0	0	.	Heines IV 28
0	0	0	0	0	0	0	0	0	.	Flamingo 29
0	0	.	0	0	0	.	0	33	17	Peko 31
0	0	.	0	0	0	.	0	19	19	Heines Kolben 32
0	0	.	0	0	0	.	18	86	100	Little Club 34
0	.	.	15	0	0	.	0	28	55	Hope × Timstein 35
0	0	.	0	0	0	.	0	57	87	Selkirk 36
3.3.5	1.3.7	1.1.3	5.15.22	1.4.14	1.1.3	1.3.5	3.6.12	2.4.4	2.3.8	weight

This has been done with the more confidence, as the higher values of Leda, Heines IV, Flamingo and Alba are explained in part by the earliness of the artificial epidemic in race nursery 0012, these varieties, and especially Leda, becoming more and more resistant towards the end of the growing season (fig. 24.42). The supposition that an Alba-Leda race exists (ZADOKS, 1957) has not been corroborated by more recent experience. The final position of the Leda-isolates, however, has still to be elucidated.

Heines VII - Heines IV race (race B 7x; table A.24.42.d)

This race of the Rubis group is compatible with Heines VII and Heines IV and incompatible with Peko.

It is represented by one monospore culture of the *Biologische Bundesanstalt*, Braunschweig, tested in 1956 in nurseries in Braunschweig, Waterneverstorf and Schnega (all in Germany).

No epidemiologic data on this race are available.

Flamingo race (race B 54, W 12; table A.24.42.e)

The Flamingo race, of the Rubis group, is compatible with Heines VII, Merlin, Heines IV, Flamingo, Peko and Heines Kolben.

The race had been first observed in the Noordoostpolder 1958 in a Flamingo field, adjacent to a breeder's nursery containing an International Yellow Rust Trial. This situation was repeated in 1959. Isolates 8887, 9168 and 9793 have been tested in race nurseries in 1960. The resulting infection was poor, especially in the spring wheat section. This also illustrates that the Flamingo race is not very virulent. Data on Heines IV had to be discarded, as this variety could also have been infected by the spontaneously occurring Triumph race.

In the greenhouse the Flamingo race behaves as race B 54, W 12, as does the Peko race.

Peko race (race B 54, W 12; table A.24.42.f)

The Peko race, belonging to the Rubis group, is compatible with Heines VII, Merlin, Peko and Heines Kolben, but incompatible with Flamingo and Heines IV.

The identity of the Peko race is well established by five trials over three years with four isolates, one from Heines VII (8700) and three from Peko (6900, 8880 and 8901).

In the greenhouse the Peko race behaves as race B 54, W 12; this applies also to the Flamingo race.

Heines Kolben race (race B 1x, W 4; table A.24.42.g)

The Heines Kolben race, of the Rubis group, is compatible with Heines Kolben, but not with Heines VII, Merlin, Heines IV, Flamingo or Peko, though Peko shows a slight infection.

Tests have been done with a monospore culture from the *Biologische Bundesanstalt* at Braunschweig, isolate 119, in four nurseries in 1960. The nurseries differed in soil type and sowing time. The results are consistent, though the infection of trial 0009 is a bit low in the spring wheat section.

In the greenhouse the infection spectrum of this race falls between those of the classical races 1 and 9.

Chinese race (race B 27/53, W 13; table A.24.42.h)

The Chinese race is compatible with Chinese 166 and to a less degree with

Carstens V and Felix; it is incompatible with Rubis or any other field differential.

Three isolates have been tested; one is a Braunschweig monospore culture of race B 27/53, isolate 113 came from a spontaneous infection in the Wageningen rust nursery and the origin of isolate 105 is unknown.

In the greenhouse the isolates are identical and well characterized as race B 27/53, W 13.

Race B 27/53 has been found in Northern France in 1938 (BECKER, 1942) and has been present ever since. The epidemiology of this race is quite mysterious. It is present all over Europe and in the Near East, and it is frequently isolated (FUCHS, 1960). The mystery is in the fact that only few commercial varieties can serve as a carrier for this race. Accordingly, no severe epidemic has ever been related to race B 27/53 in Europe, though this race may have been responsible for recent outbursts of yellow rust in Egypt (HASSEBRAUK, 1959).

Commercial varieties, susceptible to the Chinese race, are Probus in Switzerland and Graf Toerring II and a few minor varieties in Southern Germany. In the Wageningen rust nursery Felix showed a late infection by the Chinese race as it did also in one of the race nurseries in Baarn. It is curious to see that race B 27/53 has been isolated several times in Switzerland, where the susceptible Probus is grown, but that Chinese 166-W in the Swiss International Yellow Rust Trials has never been infected. The race is frequent in the Near East and it has been isolated from several Mediterranean countries (FUCHS, 1960).

Cappelle race (race B 2x/55, W 8; table A.24.42.i)

The Cappelle race is compatible with Nord, moderately compatible with Cappelle and Staring, and incompatible with Rubis and the other differentials.

Exact information on this important race is scarce. Two breeder's nurseries in Germany 1956 were infected with a monospore isolate of race B 2x, provided by the *Biologische Bundesanstalt*. These nurseries were also infected with race B 7x. Some conclusions could be drawn from the observations, applying the subtraction technique, because the reactions to the particular isolate of race 7x were known from a Braunschweig race nursery inoculated with B 7x.

A better result was obtained by the Foundation for Plant Breeding (S.V.P.) at Wageningen, where a race nursery was inoculated with a race B 2 isolate from Braunschweig (MESDAG, 1958).

The 1957 trial 2470, lying in the middle of a Staring field, was infected by the Cappelle race and a more prevalent race, infecting Heines VII. Again by subtraction some data could be furnished. The results of the International Yellow Rust Trials Project suggest that the other field differentials are fairly resistant to the Cappelle race, but experimental proof fails. This is because the Cappelle race is difficult to cultivate in the greenhouse; it is even more difficult to start an artificial epidemic in the field with this race.

In the greenhouse the Cappelle race reacts as race B 2x/55, W 8, as does the Etoile de Choisy race.

Triumph race (race W 16; table A.24.42.j)

The Triumph race is compatible with Triumph, but not with Rubis or any other differential. Heines IV is infected with a IT = 2 and a CI = 9.

Two 1959 isolates (9775 and 9798) have been tested in race nurseries. A spontaneous infection of the race nurseries by the Triumph race provided additional information from 28 nurseries (table A.24.33).

In the greenhouse the Triumph race behaves as race W 16, as the Heines VII and Alba races.

Alba race (race W 16; table A.24.42.k)

The Alba race is compatible with Alba only.

Two 1958 isolates from well infected Alba fields (8130*b* and 8893) have been tested over a period of three years.

In the greenhouse the Alba race reacts as race W 16, indistinguishable from the Heines VII and Triumph races.

Etoile de Choisy race (race W 8; table A.24.42.l)

This race is compatible with Nord and, to a less degree, with Etoile de Choisy, Marne and Carest.

Two 1959 isolates (9–345*d* and 9547) have been tested in three trials in 1960. The infection result was poor and it was obscured by spontaneous infection of the Triumph race. Discarding those data, attributed to the Triumph infection, the remaining figures are of sufficient interest to be presented here. The CI.s of Etoile de Choisy, Marne and Carest are of the same level, the CI of Nord is higher; all of them are underestimated because of the spontaneous infection, which determined the high IL.

Justification of the distinction of an Etoile de Choisy race is not so much in the relatively poor data provided by the race nurseries, as in the data of the International Yellow Rust Trials in northern France, which show the same infection pattern as the race nurseries.

In the greenhouse the Etoile de Choisy race cannot be distinguished from the Cappelle race, both reacting as race B 2x/55, W 8.

Heines IV race (race B 7x, table A.24.42.m)

The Heines IV race is compatible with Heines IV and incompatible with any other field differential tested.

The race has been identified on the basis of a race nursery established by the *Biologische Bundesanstalt* in 1960 with a monospore culture of race B 7x. The result was somewhat unexpected.

Probus race (table A.24.42.n)

The Probus race is moderately compatible with Hope × Timstein and incompatible with any other differential.

No race nurseries have been inoculated with the Probus race. The RC is based on data from the International Yellow Rust Trials in Switzerland 1956–1960. The great variation between the AIS.a is explained by spontaneous infection of varying intensity. The data permit the description of a Swiss population. As the AIS.a from different trials and different years are very similar (an observation confirmed by the writer's careful yellow rust assessment of collections of over 100 varieties in Haag-Gams, Zürich-Reckenholz and Lausanne-Cery in 1959), it seems justified to speak not only of a Swiss population but also of a Swiss race. As the Swiss wheat culture is almost a monoculture of the compatible winter wheat Probus, the name Probus race is appropriate.

Fuchs (1960) isolated several races from Swiss samples, e.g. B 2x/55, B 27/53 and B 54. As Heines Kolben-W and Chinese 166-W have never been found infected in the Swiss Yellow Rust Trials, the races B 27/53 and B 54 cannot have

been generally prevalent. Probably the Probus race is related to the B 2x/55 group, this is also suggested by field observations: Nord, several other French wheats and Staring characteristically show a maximum DA = 4, whereas the northern German varieties as Heines VII and Merlin under the same conditions have a DA = 0. Greenhouse tests in combination with race nurseries must give the final identification of the Probus race.

Race 2x/55 (race B 2x/55, W 8; table A.24.42.o)

This race is remarkable because of its incompatibility with any differential used. Only Alba has been mildly infected.

Two monospore isolates, provided by the *Biologische Bundesanstalt* as races 2x and 55 (isolates 117 and 118), have been tested in different localities, on different soils and with different sowing times. The results were practically identical in all trials.

In the Wageningen greenhouse the races B 2x, W 8 and B 55, W 8 cannot be distinguished. Owing to their virulence to Vilmorin 23 they are clearly distinguished from the Alba race W 16.

No epidemiologic data are available on race 2x/55.

Race 7x (race B 7x; table A.24.42.p)

Race 7x is characterized by the absence of compatibility with any of the field differentials.

A monospore isolate of race B 7x has been tested in a race nursery by the *Biologische Bundesanstalt* in 1960.

Epidemiologic evidence on this race is not available.

Grecian, Iberian and Levantine populations (tables A.24.42.q, r, s)

The grouping of AIS.a from different countries into three populations is arbitrary. On closer inspection these populations can probably be split up into several distinct races. The Grecian population is the most homogeneous one. About the Iberian population nothing definite can be said. The Levantine population, combining data from Egypt, Israel and Turkey, is characterized by genes for virulence to Hope × Timstein. This variety is found to be infected in the mature plant stage in Egypt and Israel, in the seedling stage in Turkey. An Israelian isolate was compatible with Hope × Timstein in the greenhouse.

Kenya population (table A.24.42.t)

There is little reason to assume that the Kenya population here described is a racial entity. The data of the International Yellow Rust Trials have in common compatibility with Little Club, Selkirk and Hope × Timstein. The high susceptibility of Selkirk, resistant in Europe but susceptible in Egypt and Israel, is impressive. Hope × Timstein is sometimes severely infected, as in Egypt and Israel.

24.43 Field races and greenhouse races compared

Three of the greenhouse races W 8, W 12 and W 16 can be split up, each into two or three field races, some of which differ as much as the Heines VII and Alba races (table 24.43).

Some of the Braunschweig greenhouse races can also be split up into more

TABLE 24.43 Field races and greenhouse races compared. For details on individual isolates see tables A.23.5, A.23.6 and A.24.42.

greenhouse identification		field identification
Wageningen	Braunschweig	
W 4	B 1x	Heines Kolben race
W 8	B 2x B 55	Cappelle race Etoile de Choisy race race 2x/55
W 12	B 54	Peko race Flamingo race
W 13	B 27/53	chinese race
W 14	B $7xV_1$	$7xV_1$ race
W 16	B 7x B . B .	Heines VII race Triumph race Alba race
W .	B 7x	Heines VII – Heines IV race Heines IV race 7x race

. = no information available

field races, but on the other hand the greenhouse races B 2x and B 55 can be combined into one field race, race 2x/55.

The number of isolates tested is too small to give a final picture of the relation between greenhouse and field races. It is expected that as more isolates are tested, more greenhouse races will be subdivided.

24.44 The definition of a field race

The usual race definition (21) is not applicable to field races, for several reasons.

It refers to a standard differential set, but such a set does not exist in field work. Every new race will add its specific differential(s) to the existing set, and old differentials will be dropped when these are no longer useful. Field differentiation demands an open differential set, in contrast to the closed differential set of the conventional greenhouse work.

The usual race definition refers to major differences in the type of reaction. The varieties of the standard differential sets are chosen especially for their ability to produce such major differences (discriminative ability). In the field, on mature plants, there are usually only gradual differences in the infection type. IT is replaced by DA and its final transformation CI. As CI is a value, which can vary between 0 and 100, the concept of "major difference" must be defined anew.

In 24.5 it will be shown that the field races described previously are the real epidemiologic units. From the epidemiologic point of view the major difference is the difference in CI, which determines whether a race-variety combination will

give rise to an epidemic or not. The experiences recorded in 24.5 suggest that a CI $\geqslant 15$ can be regarded as dangerous.

These considerations led to the following definition: a field race is a unit distinct from other units by so high a compatibility with one or more varieties of a differential set in the mature plant stage that it may produce epidemics on these varieties but not on others.

New ideas in this definition are:

the differentiation in the mature plant stage,

the acceptance of the open differential set by omission of the word standard, and finally, the epidemiologic way of thinking in the description of the "major difference".

An alternative and more formal definition is the following: a field race is a sub-race, distinct from other sub-races of the same race, by... etc.

24.45 Specific virulence and versatility

The field races can be assigned two quantitative characters: specific virulence and versatility (table 24.45). These characters must not be seen as absolute quantities, but should be regarded as aids indicating differences and resemblances between field races.

Specific virulence is the virulence of the field race on its specific carrier variety, measured as the CI of the race and its carrier. For example, the specific virulence of the Alba race is 46 (table 24.42). When there is more than one carrier variety, the carrier must be specified, e.g. the specific virulence of the Flamingo race is 24_{Flam} and 39_{HVII}.

The versatility of a field race is measured as the number of field differentials

TABLE 24.45 Specific virulence and versatility of field races (see also table 24.42). The specific virulence is the virulence (expressed in CI) of the field race to its specific carrier variety; the versatility of a field race is the number of field differentials with a CI $\geqslant 15$.

races	specific virulence	versatility	epidemics
race 7xV_1	.	1	.
Heines VII race	41_{HVII}[1])	2	severe
Heines VII-Heines IV race	82_{HVII}	2 or 3	.
Flamingo race	$24_{Flam.}$	5	light
Peko race	37_{Peko}	4	light on Peko, severe on Heines VII
Heines Kolben race	77	2	light or locally important
Chinese race	92	2	.
Cappelle race	$20_{Capp.}$	2 or 3	moderate (severe on Nord)
Triumph race	47	1	locally severe
Alba race	46	1	locally severe
Etoile de Choisy race	c.$20_{Edc.}$[2])	$\geqslant 2$	light
Heines IV race	75	1	local and moderate
Probus race	$42_{Prob.}$	1	moderate to severe
race 2x/55	.	0	.
race 7x	.	0	.

. = no information available

[1]) = specific virulence to the main carrier, which is not necessarily the most compatible variety

[2]) = estimated value, based on observations from International Yellow Rust Trials

which the race can attack. For reasons explained later (25.22) the pairs Rubis – Little Club and Heines VII – Merlin have each been taken as one variety.

A variety is regarded to be liable to attack by a race when their CI $\geqslant$15. Though this limit is arbitrary, it is based on the expectation that race-variety combinations with $10 < CI < 20$ can show occasional epidemics (24.52).

It is interesting to study the behaviour of field races on seedlings in the greenhouse. In routine work isolates are transferred from sporulating to healthy plants continuously. The time in days between successive transfers is called the "transfer time". This transfer time shows great variations according to environment, isolate and race, and extraneous factors such as holidays. Nonetheless, as an isolate is transferred as soon as possible, the transfer time is an indication for the virulence of the isolate.

In routine work the number of leaves inoculated and the number of leaves sporulating as a result of inoculation were noted down at each transfer. From these notes the "percentage of success" of the inoculation was computed. Here too there were marked variations, which were partly due to racial differences between isolates. Differences in the handling of isolates by the technician can be practically ruled out, data being derived from the routine work of keeping the isolates alive.

In fig. 24.45 the average transfer time and the percentage of success have been plotted for a number of field races. The field races were represented by one to four isolates, the number of plants tested varied from 218 to 960. Only data of

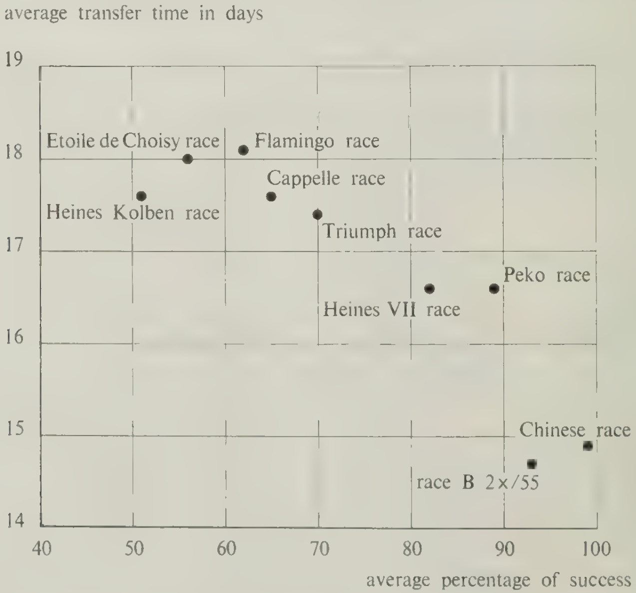


FIG. 24.45 Relation between the average transfer time in days and the average percentage of success of the inoculation. Field races have been tested in the greenhouse on seedlings of *Triticum dicoccum tricoccum* during the year 1960. There is a trend from moderate virulence (left upper side) to high virulence (right lower side).

1960 have been used as in this year irradiation was adequate. For all isolates *Triticum dicoccum tricoccum* was used as a host which reacted with well sporulating type 4 lesions to all isolates.

There is a remarkable trend in the virulence of the various field races when tested in the greenhouse on the same host variety under semi-constant conditions. The trend does not tell us anything of the behaviour of the races in the open; in the greenhouse, however, the trend is quite real, as the races in the upper left corner are more difficult to work with and to identify and are more susceptible to environmental fluctuations than the other races.

The signalized trend can also be seen in the resistance of the various field races to the disturbances accompanying vacuum storage of uredospores; some races survive vacuum storage better than others.

24.5 Field races and epidemics

24.51 The reconstruction of the past

An attempt to reconstruct the past on the basis of a few recent experiments contains an element of speculation.

Nevertheless, the challenge has been accepted, because growing insight into the history of epidemics and increasing understanding of physiologic specialization in the field influenced each other.

The story of yellow rust epidemics reaches far back into the past (table A.24.51), but in this paragraph the discussion will be restricted to epidemics caused by races about which adequate data are available.

24.52 The epidemics

The Carstens V epidemics

Carstens V is a German variety, commercialized in 1921. It has been widely cultivated in Germany and in the Netherlands. During the epidemics of 1926 and 1927 in northern Germany and the following years 1928 and 1929, Carstens V was resistant; in later years it was found to be susceptible (Gassner & Straib, 1932).

Race nurseries were established by Küderling (1937) in 1933. He made notes with a scale from 0–5, using Michigan Bronce as a standard. These notes have been revised, using only notes taken after 1st June from inoculated plants; the notes from each race-variety combination have been averaged and multiplied by 10. The resulting data, entered in table 24.52.a are comparable to ARDAP.s.

Isolates Danzig and Kitzeberg 32 are similar in their marked compatibility with Carstens V in the mature plant stage. They belong to a race, which we may call the Carstens V race. Straib (1936a) thought that the greenhouse race 7 was responsible for the Carstens V epidemics. Race 7 was first found in Svalöf (Sweden) 1931; the related race 5 has been found in Schlanstedt (Germany) 1930 (Gassner & Straib, 1933). Between 1934 and 1939, race 7 was repeatedly found in the Netherlands, no doubt associated with Carstens V (Becker, 1942).

In the years 1935 and 1936, Carstens V was mildly infected nearly everywhere between the rivers Weser and Elbe, in contrast to the dry year 1934 when yellow rust infection was much reduced (Straib, 1939a). In the years 1946 to 1952, Noll (1955) found race 7 to be the predominant race in Germany, in relation with the widespread Carstens V. In 1949 Carstens V had still yellow rust in the

northern Netherlands (Friesland; DANTUMA). Race 7 has been found in field isolates up to 1954 (FUCHS, 1960), but the race was no longer related to Carstens V.

The Heines Kolben epidemics

In the summer of 1927, von Rümkers Sommerdickkopf was found to be infected by yellow rust in the yield trials of the breeder STRUBE at Schlanstedt (Germany), though this variety had always been resistant in the field and was still resistant in the Braunschweig rust nurseries in 1927 (GASSNER & STRAIB, 1930b).

In the summer of 1930, von Rümkers Sommerdickkopf and Heines Kolben were severely infected in trials of the breeder HEINE at Hadmersleben and of VON RÜMKER at Emersleben, whereas at STRUBE's in Schlanstedt these varieties showed only trace infection.

In the greenhouse the hitherto resistant Heines Kolben was in the seedling stage susceptible to isolates from mature plants of von Rümkers Sommerdickkopf and Heines Kolben. The new race was called race 9, a race which sometimes mutated into race 1 (GASSNER & STRAIB, 1933). Race 1 had been isolated from the field at Klein Wanzleben in 1931.

KÜDERLING (1937) used an isolate of race 1 in one of his race nurseries in 1933. This isolate, Langenstein 31/2r, attacked the varieties Ridit, Blé Aurore, Normandie, von Rümkers Sommerdickkopf and, to a less degree, Carstens V. Heines Kolben has not been tested, von Rümkers Sommerdickkopf was highly discriminative in the mature plant stage, Carstens V was less compatible with race 1 than with the Carstens V race proper (table 24.52.a).

Apparently, von Rümkers Sommerdickkopf and Heines Kolben reacted in the same way to the new race, which as a field race will be called the Heines Kolben race. In the greenhouse the race behaved as race 1 or, more probably, as race 9. The race was relatively rare, but STRAIB (1939a) isolated it practically every year, especially from rust samples taken at Hadmersleben, the nursery of Heines Kolben.

Breeders called the Heines Kolben race the "spring wheat race", as it endangered several spring wheats, i.a. Heines Kolben, von Rümkers Sommerdickkopf, Normandie, Saumur, Blausamtiger Kolben and Blé Aurore (seedling reactions also in BECKER, 1933 and 1942). The race seems to have been present consistently up to World War II.

FUCHS (1960) isolated a race B 1x from the rust nurseries in Braunschweig

TABLE 24.52.a Results of KÜDERLING's race nurseries. Entries are transformed notes of KÜDERLING (1937), to be read as ARDAP.s.

varieties \ isolates	Alnarp	Grosny	Kitzeberg 31/2	Danzig	Kitzeberg 32	Langenstein 31/2r (race 1)
Ridit	10	5	5	5	5	35
Blé Aurore	5	0	0	5	17	28
Normandie	6	1	3	7	2	24
Von Rümkers Sommerdickkopf	0	0	0	0	0	22
Carstens V	0	0	5	38	37	18
Panzer III	4	6	0	5	9	4

and Wageningen. A Braunschweig monospore isolate of race 1x has been tested in Wageningen as isolate 119; it was identified as race W 4 showing most resemblance to STRAIB's race 9. In the field, this race was highly virulent to Heines Kolben and avirulent to Carstens V, in accordance with GASSNER & STRAIB (1930b) but not with KÜDERLING (1937; table 24.52.a). Nevertheless, the name Heines Kolben race seems appropriate. Whether the new and the old Heines Kolben race represent one and the same race or two closely related races, cannot be said with certainty.

The Joncquois epidemic

A very destructive epidemic occurred on Joncquois in the Netherlands in 1937. As no accurate data on the race involved are available, this epidemic is discussed below with the epidemics of the Cappelle race.

The Heines VII epidemics

In the years 1945 to 1947, FEEKES found severe infections on Heines VII and Merlin in sowing time experiments, but the actual beginning of the Heines VII epidemics dates from 1953.

In 1953 a mild infection of Heines VII had been observed in Zeeland (Netherlands) and in the Weser-Ems area (Germany). A control test in Braunschweig with two hundred pure lines of Heines VII with all races available gave negative results (LEIN).

In 1954 many fields of Heines VII on the islands of Zuid-Beveland and Noord-Beveland (Netherlands) were found to be moderately or severely infected. Foci occurred in Friesland, in variety trials at Hoofddorp (s'JACOB) and in the Noordoostpolder (table 24.52.b). In the rust nursery at Wageningen, Heines VII remained free of yellow rust.

In 1955 yellow rust struck Heines VII with astonishing severity over nearly all of the Netherlands (table 24.52.b) and spread over the larger part of Belgium (BROEKHUIZEN, 1955), though there the acreage of Heines VII was small. In England, at the end of the growing season, yellow rust was generally found on Heines VII and Merlin at low intensities. BATTS (1957a) identified the race present as race C 8b, which later appeared to be synonymous with the Braunschweig race B 7x (FUCHS). In 1955 race B 7x was identified for the first time and was isolated in the Netherlands from Heines VII, in Germany from Heines VII, Merlin and several other varieties.

In 1956 a focal epidemic developed, which reached the damage limit only in few fields, where rust had appeared early. FUCHS (1960) isolated races of the 7x group from Heines VII and other varieties in France, Germany, Great Britain and Ireland. Race B 54 was found in two German samples outside the area of the Heines VII epidemic. In Belgium, Heines VII was infected in variety trials in the Flemish polders.

In 1957 the epidemic on Heines VII was exceptionally early and severe. It was accompanied by young plant infections on Carstens VI, Flamingo and Peko. Sometimes Leda fields showed an infection in the transition stage. Most of these infections stopped before heading, but the Peko infections indicated that at least sometimes a race other than B 7x was involved. At Braunschweig race B 7x was isolated from samples of many North-west European countries, also from Heines VII in the Netherlands. But race B 54 was found in the Netherlands also, on Heines VII, Peko and other varieties.

TABLE 24.52.b Observations on physiologic specialization on mature plants before 1956.
The original data, obtained from breeders, have been arbitrarily transformed into values comparable to RDAP.
In the years 1948 to 1954 the Cappelle race is predominant. In 1954 the Heines VII race appears in the Noordoostpolder. In 1955 the Heines VII race is predominant, except in Versailles, where the Cappelle race is active.

field number	year	1948	1952			1954			1955										BATTS, 1957a	
	locality	Versailles[1])	Emmeloord	Rilland-Bath	Westpolder	Westpolder	Emmeloord	Versailles[1])	Waterneverstorf	Westpolder	Hoofddorp	Rilland-Bath	Emmeloord	Noordoostpolder "De Kandelaar"	Wageningen "I.P.O."[2])	Wageningen "I.V.R.O."	Versailles	races[2])	
	trial number	7120	3520	3460	3210	3210	3520	7120	2110	3210	3340	3460	3520	.	3630	.	7120	C 2b	C 8b
7	Staring	.	10	.	.	.	.	.	1	10	2	2	1	10	50	2	0	R	R
8	Nord	60	64	25	25	50	.	80	10	100	5	25	1	10	1	.	80	S	R
9	Cappelle	50	25	3	2	25	1	30	18	1	0	0	1	0	1	0	40	S(R)	R
10	Triumph	.	.	.	.	.	.	.	.	.	.	.	.	0	0	8	.	.	.
11	Heines VII	.	0	0	0	0	67	.	1	10	45	43	100	100	50	70	5	R	S
13	Merlin	.	.	.	.	1	7	.	.	50	.	73	100	75	75	100	0	R	MS

[1]) SIMON & CROISIER (1959)
[2]) artificial infection

In 1958 yellow rust on Heines VII was relatively rare. Races of the B 7x group and race B 54 have been found on samples from most North-west European countries, often on Heines VII. Four isolates have been tested extensively by the writer. Isolates 8589 and 8600 from Heines VII, belonging to the Heines VII race (W 16, probably synonymous with B 7x = C 8b), showed the infection pattern of the epidemics in 1955 and 1956. Isolate 8700 from Heines VII, belonging to the Peko race (W 12 = B 54), showed the infection pattern more prevalent in 1957 and 1958.

Apparently the 1957 epidemic, in contrast to the 1955 epidemic has been build up by two races, the Heines VII race (W 16 $\stackrel{?}{=}$ B 7x = C 8b) and the Peko race (W 12 = B 54).

In 1959 there was little Heines VII cultivated in the Netherlands. Only few yellow rust foci were found.

No isolates have been tested by the writer. According to LEIN, Heines VII and Merlin showed local infections or foci in several districts of Germany.

In 1960 there was little Heines VII grown in the Netherlands. Some yellow rust appeared late in the season. In Denmark there were local infections on Heines VII (ANON., 1960).

Yellow rust on Peko

Notwithstanding the fact that a special Peko race has been recognized, there were no severe epidemics on Peko.

The first infections on Peko have been observed in 1955 in Zeeland (Netherlands); they appeared much later than those in Heines VII (BROEKHUIZEN, 1955). In the greenhouse the Peko race behaves as B 54 = W 12. Race B 54 has been found since 1951 (FUCHS, 1956). It was found again in 1954, 1956 and in greater frequency in 1957 and later years. It has been found in most Northwest European countries (FUCHS, 1960).

The association of race B 54 to Peko is mainly due to the race nurseries. In the field, a severe infection of Peko is rare. As Peko is a spring wheat, the period available for the development of a severe attack is probably on the short side. As a crop Peko is relatively open, so that the crop dries easily after wetting by rain or dew. Consequently, the frequency of suitable infection periods might be less than in a more abundantly growing winter wheat crop. The highest infections observed were DA = 6, rarely DA = 8.

The Flamingo epidemics

A small percentage of susceptible plants has always been present in Flamingo, but the variety as a whole had a good resistance in the field.

In 1958 a severe infection was found in the Noordoostpolder on one field. The race oversummered and overwintered on this field and on the newly sown Flamingo of the adjacent field. The race involved, apparently new, was well characterized, see 24.42.

In 1959 the infection was again severe on the Flamingo field, bordering the field which had been severely infected in 1958. Flamingo fields in the neighbourhood were mildly infected. A focus, found in Zeeland, may well have been caused by the same race; here, however, the infection did not spread.

In 1960 the Flamingo race was still present in the Noordoostpolder, as one field was found to be moderately infected.

The Flamingo epidemics are interesting, as they are caused by a clearly

distinct race which, however, is not very virulent (specific virulence 24, other races usually about 40) and consequently does not spread rapidly.

The Alba epidemic

From 1937, when Alba was first commercialized, until 1957 Alba was resistant. Even in 1955 and 1956 no yellow rust on Alba has been observed (OVERLAET, 1958a). In 1957 there was an epidemic on Alba, well distinguished from that on Heines VII. The centre of the epidemic was in the Flemish polders of Belgium. In Zeeland (Netherlands) there was an initial focal infection, which later became general and severe. More to the north the infection remained localized.

In 1958 there was again an epidemic on Alba, but with lower intensity. In Belgium, several fields were found to be severely infected. In Zeeland, Alba was no longer cultivated. In the Wieringerwaard, the most northern outpost of Alba, inoculum overwintered on volunteers in the winter 1957–1958. The last remaining Alba fields showed a focal infection in 1958.

The infection pattern has been reproduced by isolates, representing the Alba race.

For 1959 few observations are available. The race disappeared together with its carrier variety, which, after 20 years of good service, had no longer any advantage, its rust resistance having been broken by the new race.

The Heines IV epidemics

The race characteristic of the Heines IV race brings back to mind an epidemic on Heines IV in the Netherlands, 1949. Heines IV, then in trial for admission to the Descriptive List of Varieties of Field Crops, was rejected because of severe rust infection in several trials and in about 50 hectares of multiplication plots. Heines VII, Flamingo and other varieties remained free of rust (information kindly communicated by FEEKES, confirmed by LEIN).

In 1948 Heines IV suffered from a yellow rust infection in Rheinland and Hessen in Germany (FEEKES).

The Triumph epidemics

In 1957 FEEKES observed localized infections on Triumph in some German variety trials. In the Netherlands Triumph was registered as highly resistant from 1951, when it was first commercialized, until 1959. In the mature stage its DA seldom exceded 2.

In 1959 a severe Triumph infection was reported from relatively isolated fields in the Noordoostpolder and in north-western Friesland. A focus was found in the province of Noord-Brabant.

In 1960 the Triumph race was spread all over the Noordoostpolder, the infection being sometimes severe; it was present in north-west Friesland and it caused an epidemic on 500 ha of Triumph in the new polder Oostelijk Flevoland.

The race involved, the Triumph race, is apparently a new race.

Yellow rust on Leda

Until 1957 Leda was known to be highly resistant to yellow rust. In 1957 there was a remarkable epidemic on Leda in Belgium and in the Netherlands, which followed the pattern of the Alba epidemic more closely than that of the Heines VII epidemic in that year. A few fields, scattered between the Franco-

Belgian border and Amsterdam, were severely infected in the transition stage. Other fields showed focal infections of varying DA. At the end of shooting the infection disappeared, a behaviour closely parallelled by that of the Leda isolate tested in race nursery 0012 in 1960.

In 1958 a few localized Leda infections have been reported (HULSHOFF, 1958).

In 1959 there were a few localized Leda infections, e.g. in north-western Friesland (International Yellow Rust Trial 3240, isolate 9791*b*) and in the province of Limburg (rust survey of the Plant Protection Service). The Frisian Leda infection was interesting because Leda, Alba and Heines VII were infected in trial 3240, situated in the midst of a Leda field with severe but localized infections.

These data on Leda have been assembled as they have several pecularities in common. They are, however, too inconsistent to allow the distinction of a special Leda race. They demonstrate the difficulties encountered in the attempt to give an experimental reconstruction of recent race history.

The epidemics of the Cappelle race

The Cappelle race has a long history, as can be seen from table 24.52.b. In this table, observations from years before 1956 have been summarized after somewhat arbitrary transformation of the original observations into values comparable to RDAP.s. Data are derived from SIMON & CROISIER (1959), an inquiry on yellow rust in 1955 by the Netherlands Grain-Centre, field books of private breeders and BATTS (1957a). For the sake of comparison the original observations have been transformed by inevitably subjective methods; the resulting data must be handled with caution.

In 1948 the race was present in Versailles (France); in 1951 it was found on French varieties in Denmark (ANON., 1951). In 1952 Cappelle was infected in some parts of the Netherlands and a particularly severe infection on Nord occurred in Eastern England (BATTS, 1957b). In 1953 attacks on Nord were recorded in Denmark (ANON., 1953). In 1954 the race was present in Versailles and in the Netherlands (but not in the trial 3520, where the Heines VII race dominated, see table 24.52.b) and locally severe on Nord and Cappelle in England.

In 1954 BATTS (1957a, b) recorded a severe infection, apparently by the Cappelle race, from the Dundee area in Scotland.

In 1955 the race was active in Versailles (France), Waterneverstorf (Germany; probably due to artificial infection) and in the Netherlands, where it was poorly represented by the trials 3460, "de Kandelaar" and 3630, the other trials being infected by the Heines VII race. In Scotland, in the Lothians, Cappelle showed a late infection on the heads (BELL). In 1955 there was a destructive epidemic on Nord but only moderate infection on Cappelle in Denmark, where these varieties were widely cultivated (BROEKHUIZEN, 1955; ANON., 1955).

In later years the International Yellow Rust Trials gave evidence of the Cappelle race. In 1956 rust nurseries have been artificially inoculated with a Braunschweig isolate of race B 2x. In 1957 there was a moderate infection on Staring; the writer also saw focal infections on Cappelle in Eastern Ireland. In 1959 there were foci in fields and Yellow Rust Trials in Northern France (trials 7010, 7140 and 7220), Belgium (trial 4110), England (trial 5220) and in the Netherlands (Noordoostpolder).

The old race 2 is known from 1929 onwards; it was found in French samples from Noissy (Gassner & Straib, 1933) and its presence in northern France throughout the years was shown by greenhouse and field tests (Becker, 1942). From 1955 onwards Fuchs (1960) isolated race B 2x, which is probably identical with Straib's race 2. Batts (1957a, b) thought race C 2 responsible for an epidemic on Nord in Eastern England; in the same year he found a biotype C 2b, which also attacked Cappelle. Race C 2 has not been found since 1953. Whether this change is due to a sudden change of biotypes, as Batts suggested, or to a minor change in observation and identification techniques, is not known. Confusion may arise in that Nord is so much more susceptible than Cappelle in the greenhouse as well as in the field. The 1954 epidemic in Scotland on Cappelle, Eclipse and Nord was due to race C 2b.

Whether or not the very severe epidemics on Joncquois in northern France 1936 (Herzog), the related epidemics on Benoist 40, Joncquois and Vilmorin 27 of 1937 and 1938 in the Netherlands (Droogendijk, 1937; van der Zaag, 1956) were due to a race of the group B 2x/55 ≟ C 2 ≟ C 2b ≟ W 8 cannot be said with certainty, but in view of the genetic relations between the varieties this is not improbable. Simultaneous infection of Joncquois and Jubilé is known from local Danish outbursts of yellow rust (Anon., 1945, 1946). Long term continuity of a race group specialized on French wheat varieties is indicated.

The Probus epidemics

Probus is a Swiss bred winter wheat used nearly everywhere in Switzerland. When introduced, it was resistant to yellow rust, at least in Switzerland itself. Within a few years a race did specialize on Probus, practically incapable of attacking other commercial wheats. The annual epidemics are sometimes severe, but the damage is usually small (Kobel).

The Etoile de Choisy epidemics

Infection on Etoile de Choisy and Marne has been found in 1957 at Cappelle (France), on Etoile de Choisy in the Netherlands (trial 3450) and on the same variety in Germany (trial 2310).

In 1958 traces of yellow rust have been observed on the stem leaves of Marne at Cappelle (Herzog).

In 1959 the writer saw a severely infected field of Etoile de Choisy at Versailles (France) and focal infections all around Paris, Estrées-Saint-Denis and Reims. Focal infections were present on Marne at Cappelle. A real epidemic has not yet occurred, though the race seemed to be widespread in France. Infections on Etoile de Choisy have also been reported from mid-western France.

1960 data from the trial 5620 at Plas Gogerddan (Wales) suggest that the Etoile de Choisy race jumped over from France to Wales, a fact the more remarkable as there is little wheat grown in Wales.

24.53 General aspects of race epidemics

Usually the commercial varieties, new to a country, are resistant in that country at the time of their introduction. After a period, varying from 0 to 20 years, a new race may appear which causes a more or less heavy attack, localized to a few fields or trial plots. Such an attack can easily remain undiscovered.

Once a race has established itself, it remains with a variable amount of in-

oculum, the variations being dependent on the virulence of the race, the weather and the intensity of cultivation of the carrier variety. Some races disappear together with their carriers, as in the case of the Carstens V and Alba races. Others are not sufficiently virulent to spread, as seems to be the case with the versatile Flamingo race. The frequency and the intensity of the infections caused by the Heines VII and Peko races diminished with decreasing acreage of Heines VII, although the amount of rust has also been influenced by a few unfavourable summers. Sometimes the rust race disappears as soon as the wheat is no longer grown in the danger area; Carstens V and Heines IV are still grown locally in Germany (Heines IV in 1958 about 80,000 ha.), but no recent yellow rust attacks have been recorded.

A "flaring up" or "explosion" of a new race is possible only under very favourable weather conditions over an extended period, combined with a high intensity of cultivation of the carrier variety over a large area. The Heines VII race exploded in this way in 1955, spreading over North-west Europe. The Triumph race, equally virulent, did not explode because of the extremely dry weather in 1959 and perhaps also because of a smaller acreage of the carrier variety.

25 GENETIC ASPECTS OF COMPATIBILITY

25.1 Different forms of resistance

The different growth stages and organs of the wheat plant can differ widely in their resistance. Differences between seedling and mature plant, represented by primary leaf and stem leaves, are frequent, but differences between stem leaves, stems and ears occur also.

25.11 The primary leaf

The most conspicuous gradient of resistance in the primary leaf is the gradient represented by the infection types from i to 4. The degree of resistance may be at any level of this scale, the reaction of the inoculated plants may be homogeneous or not, variable according to environmental conditions or not.

The seedling resistance is a complicated affair. In table 25.11 the frequency distributions of the infection types are given for five varieties, more or less compatible to race W 8. Vilmorin 23-W shows a skew U shaped distribution, indicating that it is compatible with race W 8, with the restriction of a high

TABLE 25.11 Frequency distribution of infection types on primary leaves of five varieties, inoculated with race W8. Data from the Wageningen greenhouse, 1960. Readings taken around the 18th day after inoculation.

varieties	infection types						n
	i	0	1	2	3	4	
6 Vilmorin 23-W	26	1	1	5	2	65	84
25 Staring-W	16	4	0	18	2	60	50
34 Nord-W	10	10	4	27	0	49	51
14 Vilmorin 27-W	17	7	9	25	6	36	99
13 Cappelle-W	11	33	24	28	0	4	72

n = number of plants tested

percentage of escapes. On the other end Cappelle-W has a skew dome shaped frequency distribution, with a median value of IT = 1. Nevertheless, in rare cases Cappelle-W responds with an IT = 4, which indicates that Cappelle's seeming resistance may be due to unknown environmental influences. The other varieties are intermediate; Staring-W seems to be useful as a supporting variety to Vilmorin 23-W.

The phenomenon of a high percentage of i types, demonstrated in table 25.11 by the combination Vilmorin 23-W – raceW8, is partly variety specific, partly race specific. This phenomenon is not due to the genetical impurity of the varieties. The variety specific aspect is called "responsiveness", a variety showing a high percentage of i types being not very responsive to inoculation. The cause of these differences in responsiveness has not been investigated. The percentage of i types, due to race specific factors, is a measure of the virulence of the race (24.45).

Another gradient is that of the time necessary for the development of a type 4 lesion. Variations between 12 and 20 days occur. The length of this period depends on the variety (Spaldings prolific and Rouge prolifique barbu being slow and *Triticum dicoccum tricoccum* being quick), on the virulence of the race (race W 13 being quick and race W 8 being slow) and on the environmental conditions, among which light intensity is important.

25.12 The stem leaves

The resistance of the stem leaves is determined by a complicated mechanism involving:

1. the percentage of spores on the leaf surface allowed to develop into sporulating lesions,
2. the incubation time,
3. the reaction type,
4. the speed of lesion growth, and
5. the intensity of sporulation.

Usually all these elements of the resistance mechanism are closely related.

Few experiments are available to demonstrate this point. In one experiment hassocks of twice five varieties have been inoculated with spore suspensions of each of the races B 2x and B 7x. Care was taken to give each hassock approximately the same amount of spores. The results are represented in fig. 25.12. The difference in the number of sporulating leaves is marked; the difference in the number of lesions was even more noticeable, but these have not been counted. The difference in incubation time is apparent, and it was confirmed by several other experiments. The difference in reaction type is clear. The difference in the speed of lesion growth, too, was conspicuous, but no measurements have been done. The lesion on Leda grew scarcely 1 mm. a day, whereas the lesions on Michigan Amber showed a longitudinal growth of nearly 5 mm. a day.

The reactions within this system of response to infection can be adequately assessed with IT and DA or PA, but there are other types of reaction which do not fit in so well in the usual method of yellow rust assessment.

A brown necrosis, composed of pin-point dots, can spread over a large area of the leaf surface of Heines 110, under conditions of very severe infection. Large oval discolorations, each covering several sq.cm. of leaf surface, occur

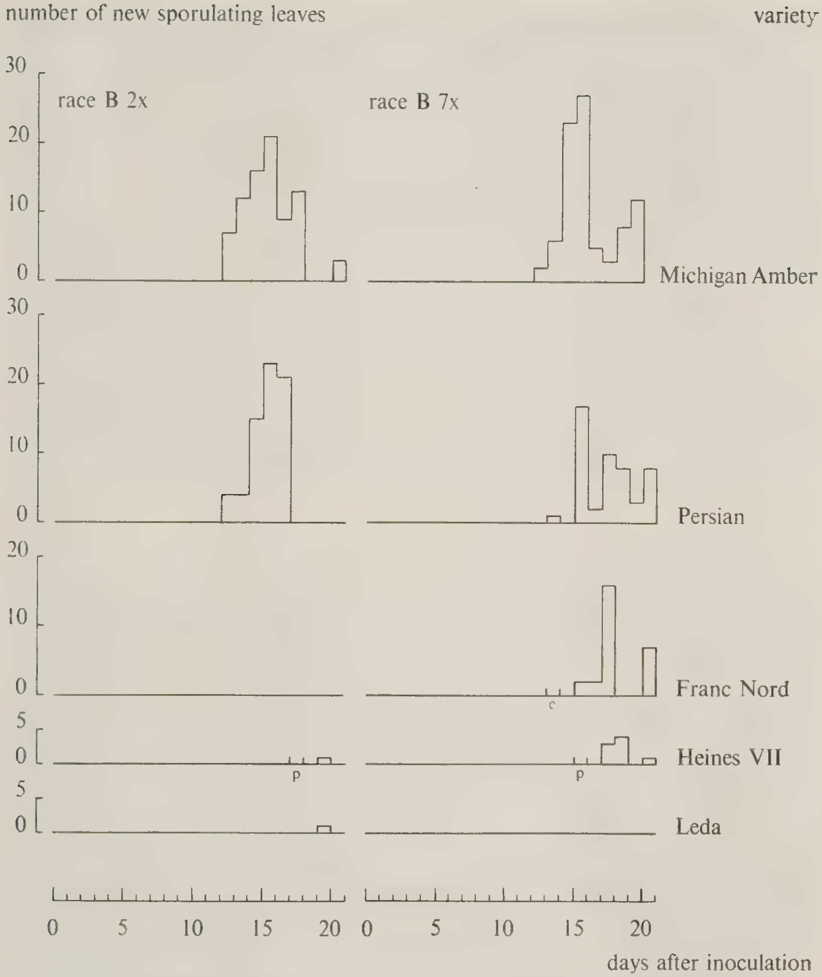


FIG. 25.12 Differences in inoculation results between varieties; field inoculations in growth stage GS = c. 8. Each day, the number of leaves starting to sporulate has been counted. The original data have been reduced to standard hassocks of 50 stems.
c = first chlorosis visible
p = first (unopened) pustules visible

sometimes on the higher stem leaves of Panter. On one occasion the writer saw a field with such ivory coloured top leaves, a curious sight. The appearance of these flecks, rare in itself, was always linked with high infection pressure of the rust. The leaves of Ile de France loose their shininess, turn yellow or ivory and wither away. For the geneticist such typical reactions may be interesting, because they suggest different mechanisms of resistance. For the epidemiologist

the main point is whether spores are produced or not; therefore, in routine work no distinction has been made between the various types of 0 reactions.

Often there is a gradient of resistance from the primary leaf to the stem leaves, the primary leaf being susceptible and the stem leaves being resistant. This gradient is frequent in the commercial varieties of North-west Europe. Mature plant resistance as contrasted to seedling susceptibility is a frequent phenomenon in cereal rust work, moreover, it is a clearly race specific phenomenon, as has been demonstrated in the foregoing paragraphs.

The reverse situation, incompatibility in the seedling stage and compatibility in the mature plant stage, is rare. An example is the combination race W13-Felix, which often gives a resistant reaction on the seedling in the greenhouse, but which is incompatible in the field until the end of the vegetation period, when it becomes compatible and shows a rapid increase in its PA.

Mature plant resistance should not be confused with heat resistance (25.15). A view on fig. 32.2.c shows that the May and June normals for the mean decade temperature computed from hourly observations vary around the greenhouse level (from c. 10 to c. 16 °C.); this implies that the mature plant resistance, as opposed to the seedling susceptibility, cannot be attributed to high temperatures only but must have another, presumably genetic component.

25.13 The stem

The stem or, more accurately, that part of the upper internode which is not covered by the sheath of the top leaf is resistant under Dutch conditions. Lesions on the stem are rare, and when they occur (e.g. Michigan Amber up to 30 % of the stem surface) they do not sporulate, the pustules remaining covered by the epidermis.

That stems can sporulate is shown by the commercial barley variety Topper; this variety sporulates heavily on the stem under conditions of severe infection with barley rust. The effect of yellow rust on the stem is an *échaudage*, equal to that of stem rust but starting at a much earlier date. A multiplication plot of Topper, severely sporulating on all parts including the stems, yielded not more than a handful of dustlike grains from 10 sq.m. Though sporulation on the wheat stem is rare in Europe (the writer has never seen it), this is not necessarily so in other regions. Literature data are not clear on this point. Santiago saw sporulation on the wheat stem in Portugal 1957; in one instance the damage was so great, that the crop was not worth harvesting.

It is not known whether the apparent resistance of the wheat stem to yellow rust is environmentally or genetically determined. The behaviour of Topper, in contrast to other barley varieties, indicates that genetic factors may be involved.

25.14 The ear, table 25.14

The ears of wheat are sometimes severely infected, sometimes not. At adequate infection levels the ears of Michigan Amber-W are infected up to DA = 10. The same is true for Rubis-W, in cases where the stem leaves are also infected. The heads of Chinese 166-W are infected up to a DA = 8, in race nurseries inoculated with the Chinese race. On the other hand, Persian-W, always susceptible in the leaves, is hardly ever severely infected in the ears.

These observations suggest that the compatibility of the ears is race specific,

Table 25.14 A comparison of the infection of stem leaves and ears at the end of flowering. Data from race nurseries. Entries are percentages of attack, PA.

organ	leaf					ear				
field race	Peko	Heines Kolben	Chinese	Alba	2x/55	Peko	Heines Kolben	Chinese	Alba	2x/55
year	59	60	60	59	60	59	60	60	59	60
trial	3675	3679	3676	3672	3678	3675	3679	3676	3672	3678
isolate	8700	119	105	8130*b*	118	8700	119	105	8130*b*	118
field number										
2 Chinese 166	0	1	100	1	0	0	0	50	0	0
4 Rubis	75	100	0	0	0	25	50	0	0	0
6 Probus	5	5	25	10	5	0	0	0	0	0
7 Staring	0	0	0	0	0	0	0	0	0	0
8 Nord	0	0	0	0	1	0	0	0	0	0
9 Cappelle	0	.	0	0	1	0	.	0	0	0
10 Triumph	0	0	0	0	0	0	0	0	0	0
11 Heines VII	25	0	0	0	0	0	0	0	0	0
15 Michigan Amber	75	100	100	75	100	5	25	5	50	50
18 Alba	0	25	0	50	10	0	0	0	0	0
20 Harvest Queen	50	100	100	75	100	0	1	5	1	25
22 Etoile de Choisy	0	0	.	0	0	0	0	.	0	0
26 Persian	50	75	75	50	75	0	0	0	0	0
34 Little Club	.	100	0	.	0	.	10	0	.	0

but that the compatibility of the ears is not always linked with that of the stem leaves.

In most of the commercial varieties of North-west Europe the ears are rarely infected. As in the exotic varieties of the Wageningen rust nursery, e.g. Michigan Amber and Rubis, infection of the heads is usual, it is presumed that the non-infected condition is mainly due to genetically determined resistance and not in the first place to environmental effects. Even during severe epidemics of Heines VII, Alba and Triumph no important infection of the ears was seen; Bell, however, reported severe infection of the ears of Cappelle from Scotland 1955.

Kobel drew the writer's attention to the Swiss winter wheat Mont-Calme 245, in which the heads are more susceptible than the stem leaves. This was corroborated during a trip into an Alpine valley, where Corbaz and the writer made the following observations on two neighbour fields, one sown with Probus and one with Mont-Calme 245:

Mont-Calme 245/Le Châble (Switzerland)/92981/29-6/11.1/4/4F5E4-5
Probus /Le Châble (Switzerland)/93011/29-6/11.1/4/5F8E3

The American variety Chul shows a reaction pattern comparable to that of Mont-Calme (Humphrey e.a., 1924). Straib (1937) mentions Garnet to be resistant in the stem leaves and susceptible in the ear to race 7; Orjuela (1956) reports a similar effect from the variety Kenya Governor in Colombia.

25.15 Heat resistance

The acknowledgement of the fact that resistance is usually race specific does not imply that other forms of resistance do not occur. In the older German literature there has been much talk about heat resistance and summer resistance.

Heat resistance was demonstrated by Gassner & Straib (1930a), working with seedlings at different temperatures. They distinguished absolute resistance, manifest at all temperatures between 8° and 22°C., and relative resistance, manifest at temperatures over 20°C. only, the varieties being more or less susceptible at temperatures of 15°C. and lower. Newton & Johnson (1936) described the same effect, but did not name it.

In 1934 Gassner & Straib introduced the term "summer resistance", which was meant to replace the older term "field resistance". This change of nomenclature was the consequence of a comparison between the compatibility of the mature plant and the compatibility of the primary leaf at high temperature, which corresponded well over a large range of varieties tested. They even claimed: *dass die in Gewächshausversuchen erhaltenen Ergebnisse das auf den verschiedenen Sorten ungleiche Auftreten des Gelbrostes im Felde in jeder Weise zu erklären gestatten.* Though this may be true for Gassner & Straib's experiments, the term "summer resistance" is confusing, as they definitely linked it with heat resistance. The Braunschweig workers at that time did not recognize sufficiently that summer, heat and mature plants may coincide because of cosmic events only and that mature plant resistance may be race specific and genetically determined.

The last point was realized by the scientists working at Halle, and Küderling (1937) set out to investigate temperature responses of race-variety combinations at different growth stages. He concluded that some varieties showed marked field resistance, in the composition of which heat resistance and race specific resistance participated in different degrees, according to each race-variety combination.

The writer, too, experienced difficulties in distinguishing heat resistance from stage bound resistance. Rusty Heines VII is rather sensitive to heat, but the degree to which the leaves become chlorotic and necrotic depends on the growth stage of the wheat. The more advanced the development of Heines VII is, the more the race-variety combination is sensitive to heat. From the epidemiologic point of view this heat resistance, in addition to the race specific mature plant resistance, is important because a hot spell in June may stop the progress of the epidemic, thereby reducing the ultimate damage to the crop and diminishing the amount of inoculum, which infects volunteers and enables the rust to oversummer. Indeed, the effect of a hot spell in June, 1957 on the Heines VII epidemic was marked, though it is difficult to express this effect in exact figures. Newton & Johnson (1936) studied the heat resistance of seedlings and came to conclusions regarding the epidemiology of yellow rust on wheat in Canada.

In the Wageningen rust nursery 1957 several hassocks of the spring wheat varieties Jufy I and Little Club were infected with IT = 4 and DA = 8. After a few hot days the leaves of Jufy I became chlorotic, dryish in appearance, lost their sheen, and folded together turning into upright peaks. The leaves of Little Club remained turgescent and continued to sporulate. This difference in sporulation during hot weather is another example of heat resistance.

25.16 Definitions

It seem appropriate to try and redefine some of the terms used in this discussion on resistance.

The most prominent form of resistance is "stage resistance", indicating a

TABLE 25.16 Different combinations of stage or organ bound resistance. Data for primary leaves from greenhouse tests, other data from field tests and field observations.

primary leaves	stem leaves	stem	ear	remarks
+	+	+	+	rare, Topper barley
+	+	—	+	exotics, Chinese 166-W, Michigan Amber-W, Rubis-W
+	+	—	—	commercial varieties, Alba, Heines VII, Triumph
+	—	—	—	commercial varieties, Etoile de Choisy, Heines IV
•	—	—	+	rare, e.g. Mont-Calme 245

+ = susceptible reaction
— = resistant reaction
• = reaction unknown

form of resistance which is growth stage or even organ bound. "Mature plant resistance" is the most important form of stage resistance, in which the stem leaves, the stem and the ear are resistant. Other forms of stage resistance, e.g. "ear resistance" and "stem resistance", are also possible. Table 25.16 reviews the different combinations of stage and organ bound resistance. The various forms of stage resistance and their combinations can be arranged in a sequence with increasing resistance.

At one end of the sequence is the "overall resistance", the most extreme form of resistance. "Overall resistance" is the term proposed for the situation in which a variety is resistant in all growth stages from primary leaf to ear.

Heat resistance is a form of resistance which is super-imposed on stage resistance and which becomes apparent only at relatively high temperatures. Heat resistance can become manifest in all growth stages. It can be quite marked in the seedling stage but its importance in the mature plant stage has been overestimated.

"Field resistance" has been used as the sum total of stage resistance and mature plant resistance in the mature plant stage. In common language the link between field resistance and mature plants is as strong as it is inappropriate. Seedling resistance is not only a greenhouse curiosity but an epidemiologically important form of resistance, visible in the field for anybody who cares to see it. The term field resistance should therefore be abandoned.

Both stage resistance and heat resistance should be seen as race specific forms of resistance. Race non-specific resistance will be discussed in 25.3.

The applicability of the foregoing definitions of resistance outside the sphere of yellow rust on wheat has not been tested.

25.2 A genetic analysis of compatibility

25.21 Working hypothesis

In the foregoing paragraphs it was demonstrated that some genes for incompatibility manifest themselves during all growth stages, whilst other genes are manifest only in the mature plant stage. A more detailed analysis can be attempted with the available knowledge.

This analysis is based on the following working hypotheses:

1. resistance of the wheat variety is determined by two genetic mechanisms:
   one consists of major genes conditioning race specific resistance, either of the overall type or of the mature plant type;
   the other consists of minor genes conditioning race non-specific resistance, modifying the effect of the race specific genes;
2. the gene for gene hypothesis of FLOR (reviewed in ZADOKS, 1959) is valid for the race specific resistance.

25.22 The analysis

Table 24.42 has been redrawn to attempt a PERSON analysis (PERSON, 1959), see table 25.22.a. The universally compatible variety is Michigan Amber, the universally compatible race is not present. Six races are compatible with one variety apart from Michigan Amber, seven varieties are compatible with one race only. Consequently, at least seven independant loci for compatibility must

TABLE 25.22.a PERSON analysis of data from table 24.42. This table is an attempt to make a PERSON analysis (PERSON, 1959) of the mature plant reactions. The lack of symmetry in the table is a consequence of the incompleteness of the available information. For explanation see text.

varieties \ races	Flamingo race	Peko race	Heines VII–Heines IV race	Heines VII race	Heines Kolben race	Cappelle race	Etoile de Choisy race	$7xV_1$ race	Heines IV race	Chinese race	Triumph race	Alba race	Probus race	races 2x/55 and 7x	number of compatible races per variety	number of varieties per class
Michigan Amber	s	s	s	s	s	s	s	s	s	s	s	s	s	s	14	1
Rubis, Little Club	s	s	s?	s	s			s							6?	1
Heines VII, Merlin	s	s	s	s											4	1
Heines IV	s		s						s						3	2
Heines Kolben	s	s			s											
Peko	s	s													2	2
Nord						s	s									
Flamingo	s															
Chinese 166										s						
Cappelle, Staring						s									1	
Triumph											s					7
Alba												s				
Etoile de Choisy, Marne, Carest							s									
Hope × Timstein													s			
number of compatible varieties per race	7	5	4?			3				2				1		
number of races per class	1	1	1?			4				6				1		

s = susceptible; CI ⩾ 15

be present in both wheat and yellow rust, with $2^7 = 128$ possible phenotypes. Only 14 phenotypes of both host and parasite are known, a number so inadequate that an ordinary Person analysis cannot be attempted.

As it seemed useful to incorporate the seedling reactions in the analysis, a modified approach has been tried. The analysis is demonstrated with an example, see table 25.22.b. In each race-variety block of the table two signs have been entered, the left upper sign for the mature plant reaction, the right lower for the seedling reaction.

In the field Heines Kolben and Peko are compatible with the Peko race and incompatible with the Chinese race. This suggests that Heines Kolben and Peko have a gene in common, conditioning resistance to the Chinese race and susceptibility to the Peko race. This gene is also active in the seedling; it is a race specific gene conditioning overall resistance and susceptibility; it has been called B. The gene for virulence in the Peko race, compatible with B, has been called β. Gene β is avirulent to Chinese 166, consequently this variety is protected by another gene, called L, conditioning overall resistance. The resistance of gene L can be broken by the compatible gene for virulence λ in the Chinese race, but λ is avirulent to B. The Peko and the Chinese race have no genes in common, but both are compatible with Michigan Amber, which lacks genes for resistance.

When testing Heines Kolben and Peko in the greenhouse with the Heines Kolben race, their reactions are found to be identical with those obtained with the Peko race. Again, Heines Kolben and Peko have a gene in common, which Chinese 166 has not. This gene might be gene B, a supposition not yet proved but accepted as the simplest explanation available and supported by the genetic relation between the varieties: Peko = Peragis × Heines Kolben. This implies, however, that the Heines Kolben race possesses gene β. The mature plant reaction of Heines Kolben and Peko to the Heines Kolben race differs from that

Table 25.22.b Example of a modified Person analysis for overall and mature plant genes. Explanation in text.

races / varieties	Heines Kolben-race	Peko-race	Chinese-race	•
Michigan Amber	+ / +	+ / +	+ / +	—
Heines Kolben	+ / +	+ / +	— / —	B
Peko	— / +	+ / +	— / —	Bc
Chinese 166	— / —	— / —	+ / +	L
•	β	βγ	λ	genes

In each race – variety block:
left upper sign-mature plant reaction
right lower sign-seedling reaction
+ = compatibility
— = incompatibility

TABLE 25.22.c Modified PERSON analysis for overall and mature plant resistance. Explanation in text.

varieties \ races	genes	Heines Kolben	Peko	Heines VII	Flamingo	Heines VII Heines IV	Heines IV	7xV1	Chinese	Cappelle	Etoile de Choisy	2x/55	Alba	Triumph	Probus	7x
		αβμ ν	αβγ δφν	αδν φξ	αβγ δεϰ νφ	αδϰν	ϰφ	α	λφ	ζμν	ζμπ	μ	φρν	ϰφ σν	φτ	φ
Michigan Amber		+ / +	+ / +	+ / +	+ / +	+ / +	+ / +	+ / +	+ / +	+ / +	+ / +	+ / +	+ / +	+ / +	+ / +	+ / +
Rubis, Little Club	a	+ / +	+ / +	+ / +	+ / +	• / •	— / •	+ / ±	— / ±	• / —	— / —	— / —	— / —	— / ±	— / •	— / •
Heines Kolben	B	+ / +	+ / +	— / —	+ / +	• / —	• / —	— / —	— / —	— / —	— / —	— / —	— / —	— / —	— / •	— / —
Peko	Bc	— / +	+ / +	— / —	+ / +	— / —	• / —	— / —	— / —	— / —	— / —	— / —	— / —	— / —	— / •	— / —
Merlin, Heines VII	Ud	— / +	+ / +	+ / +	+ / +	+ / +	— / •	— / —	— / —	— / —	— / —	— / —	— / ±	— / ±	— / •	— / •
Flamingo	eX	— / —	— / —	— / +	+ / +	• / •	— / •	— / —	— / —	• / —	— / —	— / —	— / —	— / —	— / •	— / •
Heines IV	k	— / +	— / +	— / +	+ / +	+ / •	+ / •	• / +	— / +	• / +	• / +	— / +	— / +	± / +	— / •	— / •
Chinese 166	L	— / —	— / —	— / —	— / —	• / —	• / —	— / —	+ / +	— / —	— / —	— / —	— / —	— / —	— / •	— / —
Vilmorin 23	M	— / ±	— / —	• / —	— / —	• / —	• / —	• / —	— / —	• / +	• / +	— / +	— / —	• / —	• / •	• / —
Staring	Mn	— / +	— / —	— / —	— / —	— / •	— / •	— / —	— / —	+ / +	— / +	— / +	— / —	— / —	— / •	— / •
Nord	Mz	— / ±	— / —	— / —	— / —	— / •	— / •	— / —	— / —	+ / +	+ / +	— / ±	— / —	— / —	— / •	— / •
Cappelle	Mn	— / —	— / —	— / —	— / —	— / •	— / •	— / —	— / —	+ / +	— / +	— / —	— / —	— / —	— / •	— / •
Etoile de Choisy	p	— / +	— / +	— / +	— / +	— / •	— / •	— / +	— / +	— / +	+ / +	— / +	— / +	— / +	— / •	— / •
Alba	r	— / —	— / ±	— / ±	— / +	• / •	— / •	— / ±	— / —	• / —	— / —	— / +	+ / +	— / ±	— / •	— / •
Triumph	s	— / +	— / +	— / +	— / +	• / •	— / •	• / —	— / +	• / +	• / +	— / +	— / +	+ / +	— / •	± / •
Probus	f	— / +	+ / +	+ / +	+ / +	• / •	+ / •	• / +	+ / +	• / +	• / +	— / +	+ / +	+ / +	+ / •	+ / •
Hope × Timstein	T	• / —	— / —	• / —	— / —	• / •	• / •	• / —	• / —	• / —	• / —	— / —	— / —	— / —	± / •	— / •

\+ = compatibility ± = intermediate compatibility
— = incompatibility • = no data available

In each race-variety block: left upper sign - mature plant reaction
right lower sign - seedling reaction

of the Peko race, as mature Peko is incompatible with the Heines Kolben race. Consequently Peko has more factors for resistance than Heines Kolben, and the Peko race has more factors for virulence than the Heines Kolben race. As this is visible in the mature plant stage only, Peko must have a gene for mature plant resistance, called c, and the Peko race must have a compatible gene called γ; c fails to Heines Kolben, γ fails to the Heines Kolben race. Whether or not Chinese 166 possesses gene c, cannot be concluded from the available evidence.

Table 25.22.c has been constructed on the same principles, using all data present. Genes conditioning overall resistance, have been indicated with capitals; genes conditioning mature plant resistance have been indicated with lower case letters.

Table 25.22.c is an abstract of the tables A.23.5 and A.24.42. On the basis of the available data a genic system has been drawn, but this should be regarded as tentative. A definite proof of the genic system can be given only by hybridization experiments. None the less, some salient features may be mentioned.

Varieties with only overall resistance are rare (Chinese 166 and Heines Kolben). The gene for virulence to Heines Kolben is present in at least three races. Exclusive mature plant resistance is less rare (Etoile de Choisy, Heines IV, Probus and Triumph). Genes for virulence to these mature plant resistances are present in the compatible races. At least three races have a gene for virulence to the Heines IV mature plant resistance gene. Most races are virulent to the mature plant resistance gene of Probus.

Combined resistance of the overall type and the mature plant type is present in several varieties, e.g. in Staring, which has one overall resistance gene M, broken by the Cappelle, Etoile de Choisy and 2x/55 races, and one mature plant resistance gene broken by the Cappelle race. The example of Peko has already been discussed.

Some genes seem to have an intermediate position between overall and mature plant resistance genes. Selkirk, for example, has a mature plant resistance gene, which conditions resistance to all North-west European races; in the greenhouse Selkirk never reacts with clear 0 or 4 types, but usually with IT $-$ 2^{+}. It is presumed that a mature plant resistance gene is present, exerting its influence in the seedling stage too, but only to a limited extent.

Virulence to the Rubis mature plant resistance gene is present in six races. Apparently Little Club has the same gene, but the CI of the spring wheat Little Club is lower than that of the winter wheat Rubis, due to differences in growth rhythm.

The above analytical method treats the "host-parasite system as a complete and integrated unit" (PERSON, 1959). Problems of dominance or recessiveness, gene dosage and modifier genes cannot be answered by this type of analysis. Nor is it certain that all genes of resistance will be detected. Notwithstanding the limitations of the PERSON analysis, it serves as a useful reconnaissance of the genetics of resistance against yellow rust.

25.3 Race non-specific resistance

DORST often argued that breeders should use a moderate but race non-specific resistance instead of a high but race specific resistance (also DA SILVA, 1958). Difficulties in studying this form of resistance were that it could not be expressed quantitatively and that it could not be easily distinguished from moderate race

specific resistance. The last difficulty could be met with the use of race nurseries, the first by the use of the value 100–CI as a parameter of race non-specific resistance (assuming the correctness of the working hypothesis in 25.21).

The race non-specific resistance, as measured by the value 100 – CI may be called "rest resistance". This term is based on the idea that pure race specific compatibility must result in a CI = 100, as is nearly the case with the combination Chinese 166-W – Chinese race, and that each deviation of the observed CI from the theoretical CI = 100 is due to race non-specific resistance. The situation may occur in which the rest resistance 100 – CI is far more than the race specific resistance, and then the term "rest resistance" is no longer appropriate.

The foregoing ideas on race non-specific resistance are highly speculative and must be regarded as a suggestion for a possible investigation programme.

25.4 Evolutionary tendencies in yellow rust of wheat

Though indulging in speculation again, some remarks on the topic of evolution can be made, as different levels or degrees of physiologic specialization are discernable. The physiologic specialization on the generic level in North America is less marked than in Europe (22.6) and may be interpreted as being less advanced. This can be explained by the absence in North America of a selection, accidental or not, for yellow rust resistance, whereas in Europe the process must have been going on for centuries. This age old natural selection, recently speeded up by conscious human selection and breeding, necessarily leads to more specialized forms of yellow rust, under which fall the *formae speciales hordei* and *tritici*. Naturally, such a specialization can be vizualized only on indigenous varieties, those coming from the area in which the specialization is evolving.

STRAIB's protests (STRAIB, 1935, 1936a, c) against the *formae speciales* come mainly from the fact that he tested scores of exotic varieties. Such tests, however, are irrelevant, because specialization within a certain area proceeds only on, and in dependance on, native varieties. Moreover, STRAIB's greenhouse tests with seedlings are irrelevant, because the main genetic barrier to the survival of the rust is the mature plant, in which overall resistance, mature plant resistance, heat resistance and non-specific resistance act together to keep the rust population down. In other words, the selection pressure is exerted by native varieties only and is strongest in the mature plant stage. Specialization tests should acknowledge this evolutionary concept.

Specialization of the wheat races seems to go in different directions in different continents; this is apparent when the data from China, Kenya and South America are compared with those of Europe. But even within Europe there are different lines of evolution, linked with different lines of breeding, in the wheat as well as in the rust. The French winter wheats form a closely interrelated group, and, as far as the evidence goes, their reactions to yellow rust are related too. Many are highly resistant to the Rubis – Heines VII group of races, show at most a DA = 4 with the Probus race, and are more or less compatible with the W 8 race group, especially in the greenhouse.

The North German winter wheats, mainly those of the breeder HEINE, form another group of varieties, attacked by an interrelated group of rust races. The "spring wheat rust", virulent to a group of German spring wheat varieties probably descending from common stock, has already been referred to (24.42).

The micro-evolution of the rust races evidently follows that of the wheats, in accordance with the ever-changing fashions in the theory of breeding.

The latest fashion of exchanging highly resistant parents, with possibly race specific resistance, between countries and continents may stop actual trends of micro-evolution and eventually start new trends. To the contemplative pathologist the ever changing scene of breeding and epidemiology is a fascinating spectacle.

26 DISCUSSION

The predominant thought in this chapter is that the rust, in order to survive, has to overcome ecologic and genetic barriers. The genetic barriers, set up by nature or by man, and their effects on the rust are the subject of this chapter. The resistance of the mature plant, either of the overall or of the stage bound type, is the most important barrier to survival of the rust.

Centuries of natural selection have led to a diversification of the yellow rust species into *formae speciales* (ERIKSSON, 1894). The reality of these taxonomic units, in American literature called varieties, has been the subject of some controversy. Most research has been done in Braunschweig, unfortunately with irrelevant material (25.4). In later work STRAIB (1937) changed his position somewhat, stating that many races had a specific host, either wheat, barley, *A.repens* or *H.murinum*. More important than the criticism of the Braunschweig scientists is that by HUNGERFORD (1923a, b) and his associates. Data, weighing against the concept of *formae speciales*, can be found also in LU e.a. (1956) and VASIL'EVA & AZBUKINA (1955). The admirable American work brings into mind the idea that physiologic specialization is a matter of evolution. The American wheat culture is relatively young and no serious breeding for resistance against yellow rust has ever been undertaken in North America. Therefore we should not be surprised that physiologic specialization is not yet (?) far developed in North America (25.4). Apparently, physiologic specialization on the generic level is a local affair, and the statement that it is not clearly visible in North America does not imply that it is impossible in Europe.

ERIKSSON's (1894, 1896) and the writer's field observations (22) indicate that physiologic specialization on the generic level is as real as that on the varietal level. It is, however, acknowledged that the position of the *formae speciales* is not yet sufficiently clarified. Further research is needed, testing species and varieties endemic in North-west Europe with European rust isolates in race nurseries.

The physiologic specialization on the varietal level is a consequence of the selection and breeding techniques employed. The rust can develop compatibility with the overall and with the mature plant resistance genes. The importance of the hereditary mature plant resistance has been recognized by the German scientists working at Halle (BECKER, 1933, 1942; KÜDERLING, 1937), but they had not developed adequate methods of analysis at that time. In America mature plant resistance against black rust was found by GOULDEN e.a. (1928); data on mature plant resistance against brown rust have been reviewed by CHESTER (1946, p. 213). In America, however, it was usual to screen selections for overall resistance in the greenhouse. Recently mature plant resistance was brought into the limelight by DA SILVA (1958).

European wheat breeders used to test their selections in the field. Only at Halle (Germany) screening for resistance in the greenhouse has been done continuously since about 1930. After World War II the situation changed and now most of the state breeding institutes and a few private breeders screen their selections in the greenhouse. As normally the yellow rust develops rather late in the season, the field test is actually a test for mature plant resistance, a test which cannot distinguish between overall and stage bound resistance (25.1). Often the result is only a stage bound mature plant resistance (Heines IV, Etoile de Choisy, Probus), sometimes combined with overall resistance (Nord, Cappelle, Peko); overall resistance alone is rare (Heines Kolben) (25.22). It is the consequence of the widely used stage bound mature plant resistance that the greenhouse work with seedlings can give not more than a very limited answer to the problem of physiologic specialization.

It has been demonstrated (24) that the study of physiologic specialization on the mature plant is well possible, utilizing the already existing technique of race nurseries (KÜDERLING, 1937; Braunschweig station). The method of expressing the observed infection of a variety as a percentage of the maximum possible infection at the day of observation (24.2) is a new contribution. The technique of the race nurseries (14.6) with its many hazards is subject to justified criticism, nevertheless it helped to build up a system of physiologic specialization (24.42) with explanatory value for epidemiology (24.52). It also helped to obtain a deeper insight into the genetics of resistance (25).

Not only is the greenhouse work (23) of limited value for race identification, it is subject to difficulties due to the lability of the differentials (23.3). It was disappointing that the results obtained by FUCHS in Braunschweig could not be reproduced by the writer in Wageningen. This failure and the necessity of working with those differentials found to be reliable under Wageningen conditions, led to the characterization of races with letters indicating the locality of identification (23.6). These letters indicate the station of identification, each station using the standard differential set of GASSNER & STRAIB.

The races, as defined by the combined greenhouse and race nursery work, e.g. Peko race B 54, W 12, differ not only in their infection spectrum, but also in secondary characters as virulence and versatility. An attempt has been made to express such characters in more quantitative terms (24.45). STRAIB (1939a, b, 1940) found many more physiologic differences between races, and although these have no value for race identification, they may contribute greatly towards a better understanding of the race-variety-weather complex. The present writer did not attempt such studies. Instead, he tried to find a relation between his field races and recent epidemics (24.52). Although not all epidemiologic phenomena can be explained in this way, it was shown that complex situations can be analysed, e.g. two epidemics occurring simultaneously either on different varieties (Alba and Heines VII, 1957) or on one variety (Heines VII, 1958), caused by two different field races.

The genetic analysis of compatibility (25.2) itself is highly speculative. The conclusions should be seen as working hypotheses, to be proved by genetic experimentation.

That a distinction can be made between genes conditioning overall resistance and those conditioning mature plant resistance, is a valuable result (25.23).

Genes conditioning overall resistance can be found in the greenhouse, using seedlings; a conclusion not essentially different from that of STRAIB (1937) but more restricted in view of STRAIB's overestimation of the value of greenhouse work in yellow rust research. Genes conditioning mature plant resistance, a good many of which seem to exist, can be found only by combined greenhouse and race nursery work.

27 CONCLUSIONS

The occurrence of yellow rust on grasses has been investigated. There may be a few foci of wheat rust races on *Agropyrum* species, but these are rare and small, and of negligible importance to the epidemiology of yellow rust on wheat (22).

Race identification on seedlings in the greenhouse was discussed at some length. The importance of a good regulation of irradiation and humidity, during the identification as well as during the multiplication of inoculum and the growth of the test plants, was stressed. Under Wageningen conditions only four differentials were found to be reliable: Vilmorin 23-W, Heines Kolben-W Carstens V-W and Chinese 166-W. With these four differentials a temporary race identification key has been made (23).

A detailed study of the physiologic specialization on mature plants in the field has been made. A technique was developed in order to demonstrate this form of physiologic specialization. Several field races have been described. Recent epidemics have been analysed with reference to the new knowledge on physiologic specialization on mature plants (24).

The genetic aspects of race-variety compatibility have been analysed using a modification of a technique introduced by PERSON. At least two types of resistance genes are present, one type conditioning resistance in all growth stages of the wheat (overall resistance), the other conditioning resistance in the mature plant only (mature plant resistance). Both types of resistance occur in commercial varieties, with some prevalence of the mature plant type of resistance. Genes for virulence of the rust can be compatible with either type of resistance genes. A race non-specific "rest-resistance" has been described and a method for assessment has been given (25).

3 QUALITATIVE EPIDEMIOLOGY

This chapter deals with that aspect of epidemiology which tells about "how" things happen, without going too far into deeper discussion as to "how much". The life cycle of host and parasite and some of the various factors influencing host and parasite are discussed. This chapter refers to Dutch conditions unless stated otherwise.

31 TERMINOLOGY

A few generally used terms should be defined in order to reach a clear understanding of the following pages.

A disease is epidemic, when it shows marked concentrations in time and space (Gaümann, 1945). Each concentration is called an "epidemic", irrespective of the degree of concentration, the intensity of attack or the damage caused. This strictly phytopathological concept of an epidemic is wider than the more usual agricultural concept, which applies the term epidemic only when damage is done or at least feared.

Yellow rust, being at home in North-west Europe and especially in the Netherlands, is an endemic disease with an annual epidemic cycle. Using "endemic" as a noun, the continuous presence of the yellow rust over many years can be called the yellow rust endemic. Just as an epidemic has a degree of intensity, an endemic also has a degree of intensity, the difference being that whereas in the case of an epidemic only one annual cycle is considered, in the case of an endemic a large number of annual cycles is considered.

Foci are marked concentrations of a disease in time and space, as are epidemics, but on a very small scale. For technical purposes a yellow rust focus is defined as a clearly delimited area in which the rust has a degree of attack DA of at least two points higher than the DA of the immediate surroundings; the dimension of such foci is in the order of one metre.

In the present work the incubation time is defined as the time in days between infection or inoculation and the observation of the first open pustule. This is a pragmatic definition, differing from the usual one in so far as the first open pustule is not always the first symptom to be observed. The time interval between the first symptom and the first open pustule is small in comparison with the incubation time, and as this time interval has no epidemiologic significance it has been disregarded. The incubation time as defined here is identical with Gaümann's *Fruktifikationszeit*, a term which did not find its way into the phytopathological literature.

32 THE INCUBATION TIME

32.1 A field experiment

Periodically a few drills were sown to have fresh seedlings always at hand. The variety Heines VII was used throughout the experiment, except for a short period when only Jufy I was available, a variety which gave the same results as Heines VII. For inoculation plants of GS = 1 to 4 were preferred, but growth stages up to 8 could be utilized without changing the result. An isolate of the Peko race, race W 12 was used throughout the experiment. The plot was sown some way away from the other wheat trials, but in late spring and early summer spontaneous infection could not be completely avoided.

In some periods the inoculations were made daily, in others twice weekly. As a routine a small tuft of plants was inoculated with a spore suspension, but sometimes the rubbing method was used. After inoculation the tufts were covered with pots for 48 hours to form an inoculation chamber with high humidity. When these 48 hours under cover had elapsed, the tufts were left to the inclemency of the weather. The experiment ran from May, 1957 until May, 1959 and from November, 1959 until April, 1960.

Plants were inspected daily except in midwinter, when two or three inspections per week were adequate. All sporulating leaves were excised and for each inoculation date the number of excised leaves was noted at every inspection. The

observations were stopped and the observed tufts were pulled out 10 days, later 5 days, after the observation of the first open pustule. In this way the first day of sporulation became known as well as the further course of the sporulation.

The data thus obtained were not unbiased. When spontaneous infection occurred some days before the inoculation, the observed incubation time was too short by a few days. It was, however, often possible to recognize spontaneous infection with the help of control plants and such data could be discarded. The first open pustule sometimes escapes the attention, e.g. when the observer is tired, when strong winds move the leaves or when rainfall hampers observation. In such cases the observed incubation time will be some days longer than the real one. To counteract this effect a further selection of the data has been made by grouping the observed incubation times, each belonging to a different inoculation date, according to the day of observation of the first open pustule, and rejecting all but the shortest incubation time of each group; 204 observations remained. As a consequence of the selection of data the following discussion on "incubation time" really deals with the "shortest observed incubation time".

32.2 Variation in incubation time: the influence of temperature

The main variable of environment is temperature. The individual observations of the shortest observed incubation time have been plotted against the mean temperature during that incubation time. The incubation time experiment was carried out at Wageningen; the incubation time i is expressed in days. The mean temperature t during the incubation time was computed from the daily averages derived from hourly observations at standard height (2.20 m.) in De Bilt, at a distance of c. 36 km. from Wageningen. These data were kindly provided by the Royal Netherlands Meteorological Institute in De Bilt.

The relation between incubation time i and mean temperature t is not easy to define (fig. 32.2.a). No sporulation occurs below $t = 2$°C. and no incubation time is under $i = 11$ days. When $2 < t < 4$ the incubation time i is long and rather indefinite; for $4 < t < 10$ the relation of i to t is approximately hyperbolic; for $15 < t < 19$ i is more or less constant with an average value $\bar{i} = 14$.

An empirical approximation of the relation of i to t is the regression line of $y = \frac{10{,}000}{i-2}$ on t (fig. 32.2.b). In fig. 32.2.a this regression line is transformed into a reference curve. Though the reference curve is not particularly well fitted to the observations at the ends, it is adequate for the present purpose, but for values of $t \leqslant 3$ a fixed value of $i = 100$ instead of the values indicated by the reference curve has been used.

The empirically obtained reference curve shows a reasonably good fit with the observations between 5° and 15°C. Below $t = 5$°C. i becomes long but indefinite. It must be assumed that below an unknown critical temperature the fungal development comes to a stop; consequently, below the critical temperature there is no longer a relation of i to t. The variation in the length of the sub-critical periods during the winter may be partly responsible for the variation in i. At temperatures of $t \geqslant 15$°C. the reference curve indicates rather short values of i.

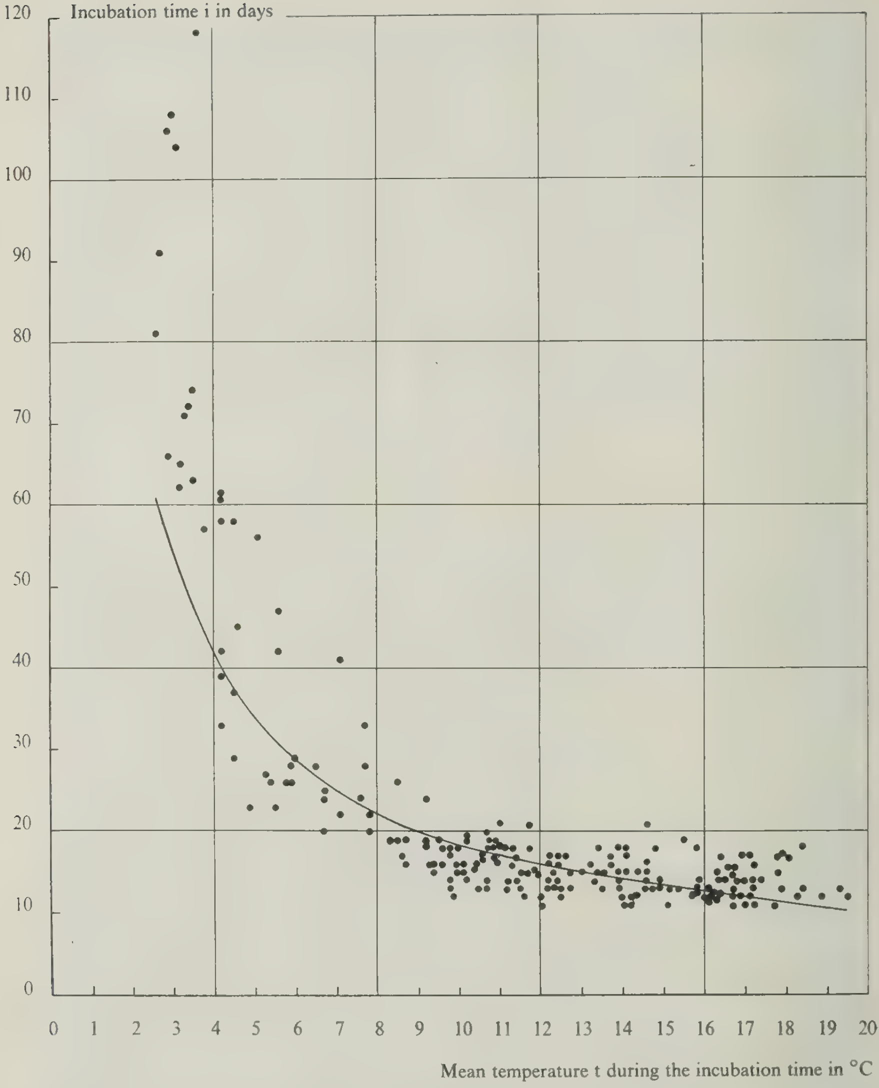


FIG. 32.2.a The relation between the incubation time i in days and the mean temperature t in °C. during the incubation time, over the years 1957–1960. The incubation time used is the "shortest observed incubation time"; dots represent individual observations at Wageningen. The mean temperature t is the mean temperature over the incubation time computed from hourly observations at the principle meteorological station in De Bilt. The regression line of fig. 32.2.b has been transformed into a reference curve.

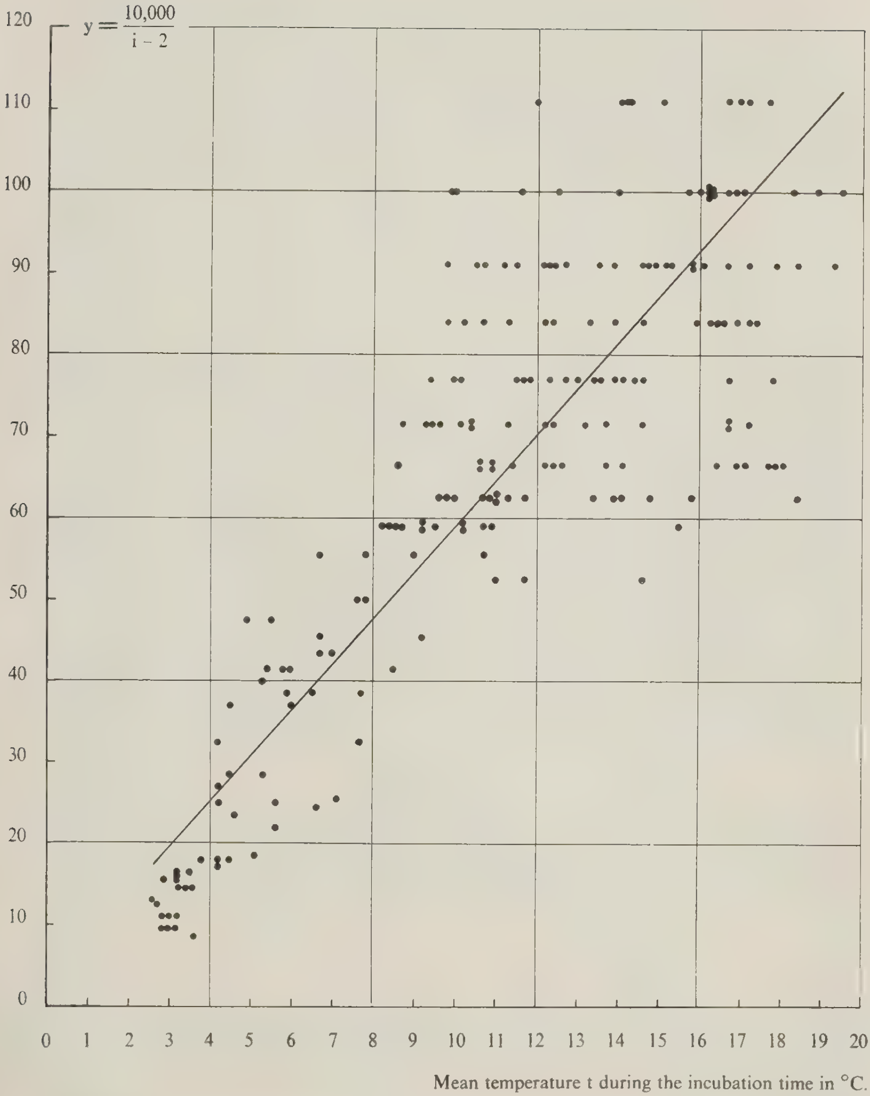


FIG. 32.2.b An empirical approximation of the relation between the incubation time i in days and the mean temperature t during the incubation time in °C., over the years 1957–1960. The regression line of $y = \frac{10,000}{i\text{-}2}$ to t has been drawn; in fig. 32.2.a this regression line is transformed into a reference curve.

The conclusion derived from the experiment and represented by the reference curve has several restrictions, but also interesting implications.

In fig. 32.2.c the decade normals N_{30} (1921–1950) for the mean daily temperature, derived from hourly observations, have been plotted; the data pertain to the principle meteorological station in De Bilt. For each decade temperature the corresponding i can be found with the reference curve. The duration of the decades, to which for the present purpose is assigned the fixed value of 10 days, can be expressed as a fraction of the variable quantity i (also in days) by using the formula $\frac{10}{i}$. The values $\frac{10}{i}$ have been plotted in fig. 32.2.c; the duration of the decades expressed in i varies from 0.1 to 0.83 i. Summarizing over the whole year, the value $\Sigma \frac{10}{i}$ gives the "maximum possible number of incubation times" – "the maximum possible number of generations" per year. It is proposed to use the term "potential number of generations per year" and the symbol N_g instead of "maximum possible number of generations per year". Instead of decade normals, monthly normals can be used for the computation of N_g. The symbol n_g can be used for the potential number of generations of a specified period.

The value n_g is useful in the analysis of the epidemiologic processes. To simplify the computation of n_g for any specified period a slide rule has been designed (fig. 32.2.d), using the data of fig. 32.2.c. The slide rule is composed of two parts, called "calendar" and "potential number of generations n_g". To find the n_g of a specified period the 0 of the upper part of the slide rule is fitted

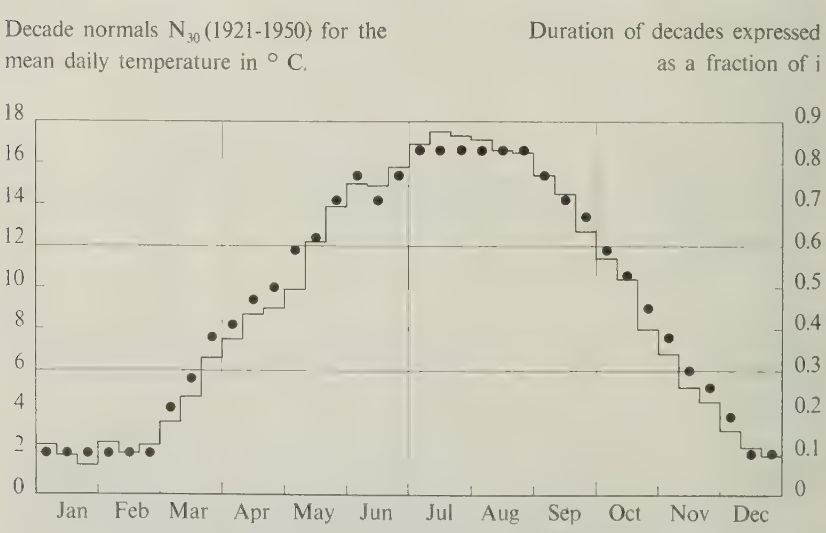


FIG. 32.2.c Decade normals N_{30} (1921–1950) for the mean daily temperature, derived from hourly observations at the principle meteorological station in De Bilt (line), and the corresponding duration of the decades expressed as fractions of i, found with the reference curve of fig. 32.2.a (dots).

TABLE 32.2 Potential number of incubation times (generations) per season

	N_g year			n_g growing season		
	Vlissingen	De Bilt	Eelde	Vlissingen	De Bilt	Eelde
1953–54	18.2	17.8	17.0	9.2	9.2	8.6
1954–55	17.6	17.4	15.9	8.6	8.3	7.5
1955–56	18.4	17.3	16.5	9.1	8.3	7.7
1956–57	20.0	19.2	17.6	10.9	10.4	9.3
1957–58	18.0	16.5	15.5	9.1	8.0	7.0
1958–59	19.8	19.2	18.2	10.2	9.7	8.9
1959–60	20.2	18.6	17.3	10.5	9.5	8.3
N_{30} (1921-50)	18.7	17.1	16.4	9.6	8.3	7.7

N_g = potential number of generations per year (1–8 till 31–7)
n_g = potential number of generations per growing season (1–11 till 30–6)

to the beginning day of the period; n_g can be read at the end day of the period.

In table 32.2 the N_g of different years and different localities has been tabulated. The localities are Vlissingen (Flushing) in the extreme south-west, De Bilt in the centre and Eelde in the extreme nort-east of the Netherlands. There is a small but consistent difference between Vlissingen and Eelde of c. 2 generations. At Eelde the yellow rust year is two generations shorter than at Vlissingen; this fact may be part of the explanation as to why the south-west is more of a danger area than the north-east. The difference is mainly in the winter temperatures, when small differences in temperature cause great differences in the building up speed of the epidemic. To evaluate the local differences in the number of generations it may be better not to use N_g, but the n_g for the growing season, from emergence till harvest. In table 32.2 n_g has been given for the period from 1st November (emergence) until 30th June (end of the increase of the epidemic).

Strictly speaking, the foregoing discussion is valid only for the combination Heines VII – Peko race, race W 12 (Peko race, CI = 50) in the Netherlands. The conclusions, however, may be applicable to other variety-race combinations with approximately the same CI (Alba–Alba race, Triumph–Triumph race,

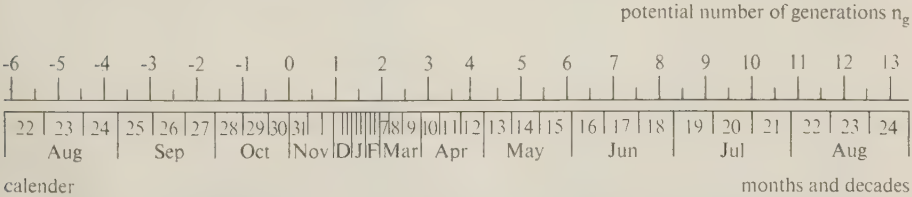


FIG. 32.2.d A slide rule for the computation of the potential number of generations n_g for any specified period, based on decade normals and corresponding decade durations (expressed in i) as represented in fig. 32.2.c.
Example: The potential number of generations n_g between emergence of a crop on 1st November and a rust observation on 10th June is required. Method: Put 0 of the upper part of the slide rule to 1ste November and read at 10th June n_g = 6.8.

Probus–Probus race) and for other wheat growing areas with a mild climate, without long term snow cover and without hot and dry summers.

It is possible that a multifactorial analysis, including temperature, daylength and light intensity, is needed to explain all variations in the length of the incubation time.

32.3 Variation in incubation time: random variations

The great variation in the length of the incubation times, even in mild periods without extreme temperatures, suggested that there are differences in susceptibility between leaves of the same age and position on the plant.

To test the hypothesis of random variation in the length of the incubation time some inoculations with a high total number of sporulating leaves were selected. For each inoculation the cumulative counts of the number of sporulating leaves on successive days were transformed into percentages of the total number of sporulating leaves; this total number was arbitrarily given the value 99 %. The percentages were plotted on probability paper and the regression line of the probit of leaf numbers (vertical axis) on the day after inoculation (horizontal axis) was computed with the method of least squares.

When the total number of sporulating leaves was sufficiently high, there was an acceptable fit of the observed data to the probit regression lines. Conse-

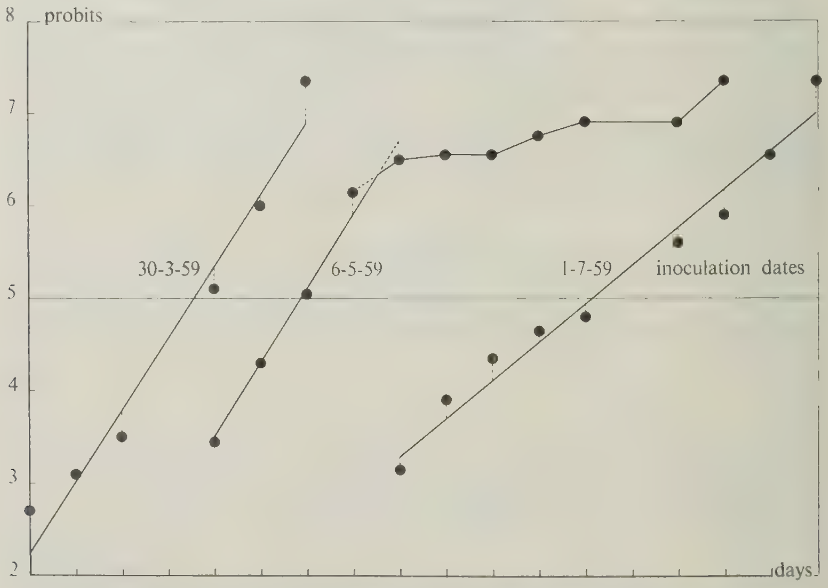


FIG. 32.3 Graphical test for random variation in the incubation times of different leaves simultaneously inoculated. Probit regression lines showing the relation between the probit of the leaf numbers and the number of days after inoculation. The leaf number is the number of sporulating leaves at the day of observation, expressed as a percentage of the total number of sporulating leaves at the end of the observation period.

quently, the hypothesis of random variation in the length of incubation times of individual leaves cannot be rejected; it is accepted as a reasonable approximation. The curve representing the daily increase in the number of sporulating leaves is, however, necessarily skew, being at the lower end delimited by the shortest possible incubation time, tapering out gradually at the upper end. This tapering out is well visualized in fig. 32.3, inoculation 6-5-1959; the long tail end of the curve has not been incorporated in the calculation of the regression line.

From the foregoing may be concluded that the "shortest observed incubation time" is a quantity situated at one of the ends of the "normal curve" representing the variation in incubation times of individual leaves, and therefore its determination is subject to great errors.

The day on which the 50 % level of the total number of sporulating leaves is attained can be determined exactly with the regression line; the period between this day and the day of inoculation will be called i_{50}, a quantity to be measured in days. The i_{50} can be estimated more correctly (in the examples with at least 4 observations) than i (necessarily only 1 observation), but the estimation involves more labour. Therefore the difference i_{50}-i has been determined only in a few selected cases (table 32.2); it varies from 1 to 5 days.

The slope of the regression lines is also variable, the tangent varying from 0.39 to 0.94. The data suggest a tendency of smaller slopes at lower temperatures. In view of the great variation in slopes, the differences between the three races inoculated to Persian are not significant.

For epidemiologic studies i_{50} would have been a more suitable quantity than i, because i_{50} represents the epidemiologically effective incubation time better than i; however, i_{50} is not easily determined in routine work. As an approximation it can be said that in the average $i_{50} = i + 3$. This implies, that a normal year with an $N_g(i) = 17.1$ has an $N_g(i_{50}) = 15.0$. To contrast i_{50} with i and to indicate its epidemiologic value i_{50} might be called the "effective incubation time".

TABLE 32.3 Variation in incubation time between leaves

variety inoculated	race	date of inoculation	i	tg	i_{50}–i	GS	n
Heines VII	Peko, W12	30–1–60	64	0.39	4.2	2	35
		11–3	33	0.49	3.7	3	88
		30–3	18	0.77	3.6	3	228
		7–4	17	0.42	4.9	4	160
		6–5–59	14	0.79	1.9	c.2	128
		1–7	13	0.41	4.2	c.2	87
		6–8–57	10	0.83	1.4	1	45
Persian	B2x	8–5–58	13	0.94	2.1	7	32
	B7x	16–5	14	0.54	3.4	7	44
	Peko, B54	16–5	14	0.54	2.7	7	55

i = incubation time
tg = tangent of regression line of probit percentage of sporulating leaves on days after inoculation
i_{50}–i = effective incubation time
GS = growth stage
n = total number of sporulating leaves per inoculation

32.4 The success of inoculation

The data of the incubation time experiment have been arranged in another way. On the fifth day after the observation of the first open pustule the number of sporulating leaves was counted for each inoculation. As the length of the inoculated tufts or drills varied from 25 to 100 cm. the counts were reduced to a standard drill length of 25 cm. The counts were arranged in groups according to the inoculation decade and the data within each decade group were averaged. The decade averages are represented in fig. 32.4.

The yearly cycle in the success of inoculation is clear. It cannot be explained without control experiments, which have not been done. The lack of success during the winter can be explained partly by the fact that spores grown in the greenhouse were not adapted to winter conditions. STRAIB (1940) proved the existence of such an adaptation, which was small but definite. The inoculum, grown during the winter without adequate irradiation, must have been of poor quality. Finally, infection may have been stopped after successful penetration by severe frosts, which killed the mycelium but just spared the leaves; a possibility demonstrated by GASSNER & PIESCHEL (1934).

In any case, the experiment indicates that in the winter the effect of a given amount of inoculum is smaller than in the summer.

33 OVERWINTERING OF THE YELLOW RUST

Just after emergence, when the primary leaf is unfolding, the new crop becomes susceptible to infection (HUNGERFORD, 1923b). Usually autumnal in-

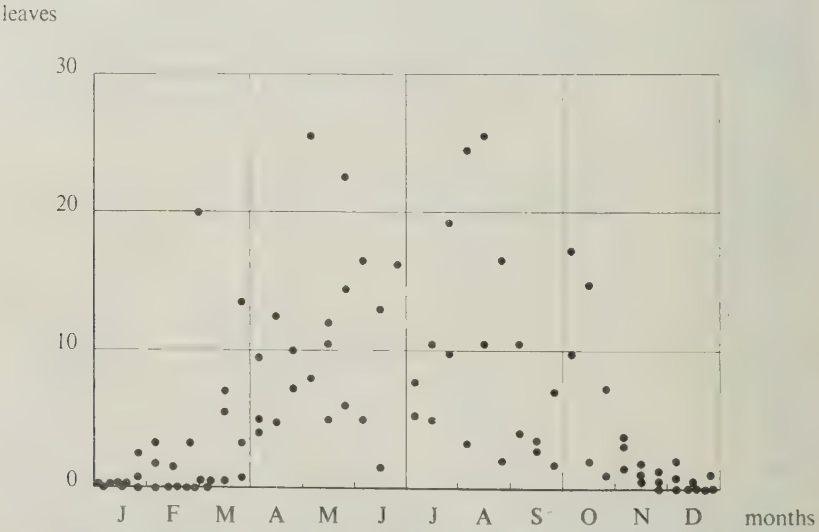


FIG. 32.4 The success of field inoculations in the course of the year. The result of a field inoculation is expressed as the number of sporulating leaves per 25 cm. drill length inoculated; these numbers have been averaged per inoculation decade over a period from May, 1957 until April, 1960.

fections become visible in GS = 2.2.3. Such autumnal infections are not infrequent but they are difficult to find. A good day's search may be compensated by finding one single infected leaf. More rarely, infection is equally and widely distributed over the crop. A DA > 1 is seldom found.

Under Dutch conditions, the infection of the newly sown crops takes place in about the first half of November. The sporulating leaves are visible from the second half onwards. Light frosts do not damage sporulating leaves. Severe frosts kill the sporulating parts of the leaves, which in a few days turn black with pink coloured dead uredinia.

This phenomenon was more closely studied in the trial field, when on 21-11-1957 a sudden night frost of c. — 4°C. occurred during a rather mild period. Seedling leaves of Alba, inoculated with the Alba-race, sporulated for a few days, but then the wounded parts of the leaves turned black, the uredosori becoming pink. One week after the night frost fresh uredosori appeared in the $\frac{1}{2}$ cm. zone adjacent to the frozen lesion, the zone in which the uredo-mycelium must already have been present at the moment of the frost. The uredo-mycelium in the not-sporulating, unwounded part of the leaf was unaffected by the frost.

This seems to be the general rule. The wounded leaf and the rust in the sporulating lesion are vulnerable; the rust in the not-sporulating, unwounded leaf is nearly as resistant to adverse conditions as the leaf itself. The writer has observed yellow rust to appear not only after periods of frost, but also after short periods of snow cover or of freshwater inundation. The mycelium in the leaf survives nearly as long as the infected, but as yet unwounded, leaf survives (GASSNER & PIESCHEL, 1934).

During the last five years it has been observed that yellow rust overwinters in the Netherlands every year anew. Why has this not been noted before? The answer to this question is not difficult. During adverse winter conditions the yellow rust lesions do not survive long. They can be found one to three days, seldom longer. Incubation periods in winter are long, e.g. ninety days. Since the presence of one single infection can be confirmed by direct observation only during three days out of ninety at the most, this gives the observer small chance indeed. The amount of yellow rust is low, at an average not more than a few lesions per ha. and these are not always at the road sides. It has happened that the writer found only one yellow rust lesion during a whole winter week's search.

Yellow rust does not necessarily overwinter on the newly sown crops. Self-sown plants, spread over unploughed or badly ploughed fields and in fields sown with Yellow Trefoil or Red Clover, may be found infected in autumn. The volunteer plants may survive into early spring, when they have not been buried by the plough in the meantime. So yellow rust may overwinter on volunteers and late tillers and infect the crop in the winter or in early spring. Both ways of overwintering occur and it is hard to say which one is the more important.

Overwintering of the rust in the form of uredospores is a hardly plausible possibility, because spores are easily washed from the leaves and yellow rust spores are very sensitive to high humidity (BECKER, 1928), not to mention repeated wettings.

34 FOCUS FORMATION

34.1 Normal focus development

Typical winter infection of a field is shown by isolated infected leaves. In some cases, it was possible to describe or to memorise the amount of infected leaves and their pattern of distribution. Coming back some time later the same amount and pattern will be found, not now of single infected leaves but of small groups of leaves, three to five closely together. These groups are beginning foci.

In some field visits it was observed that those leaves which were adjacent to sporulating leaves were covered with spores. At later visits after about six weeks, the former leaves sporulated in their turn. The shrivelled remains of the first infected leaves could nearly always be retraced, being found somewhere in the middle of the small focus. From these observations it is concluded that the dispersal of the spores within the foci was not so much by the wind carrying the spores, but by the rubbing of the sporulating leaves, moved by the wind, over their neighbours.

The further development of the focus can be reconstructed schematically, combining many observations from different dates and different fields. The first generation focus consists of one leaf only, the second generation focus counts up to ten leaves and covers a drill length of c. 10 cm.; GS = 4 to 5, the lesions can already appear on the erect leaves, offering their inoculum to the wind. The third generation focus measures c. 0.5 m. drill length with a DA = 8. The two adjoining drills are now also infected over 25 cm. but only to a DA = 6; GS = 6. Though the soil between the drills is yellow with spores, these foci are not conspicuous as they are hidden from the eye by the slightly overhanging younger green leaves.

The fourth generation foci are yellow patches of approximately 1 sq.m., easily visible for anybody who cares to enter the field. Wind dispersal of inoculum from primary foci has taken place some time previously and small secondary foci are visible throughout the field. Due to conditions of weather and microclimate, of which little is known, the further development may vary between two extremes: the foci remain strictly localised, or they extend so rapidly that the whole field is evenly infected.

Focus formation as described above in the seedling and transition stages occurs when yellow rust overwinters in the field. The same story may be reenacted during the transition stage and later. The pattern of primary and secondary foci, sometimes with single tertiary infections or tertiary foci, can be found at any growth stage.

When the early spring is dry, as occurs often in the Netherlands, the foci develop slowly and scarcely spread laterally. Younger leaves however are infected as soon as they appear and the foci spread vertically; this effect is called the "funnel effect". At the heading stage the yellow rust appears on the top leaves and the foci are clearly visible as yellow patches in a green field when seen from a dyke, a bus or any other viewing point.

When the conditions are favourable to yellow rust, only few foci are needed to infect the whole field. The most amazing example of this which the writer has seen was field 6057, a field of c. 10 ha. with one focus of c. 8 m. ø on 28-5-1956; no lesion was found in the rest of the field. On 13-6 secondary foci were visible.

On 29-6 there was a general infection of DA = 7. The development of the rust was explosive.

Heines VII/Hoek/6057/28-5/ 8 /4/+F5, ø 8 m.
13-6/10.3 /4/ 5
29-6/10.53/4/ 7

From the foregoing it is clear that the trained observer is able to read the picture which any given rust situation presents. The age of the foci can be estimated with some accuracy and conclusions on the origin of the inoculum can be provisionally drawn. In this way the field observations contribute to the understanding of the development of an epidemic.

Focus formation is not restricted to any season or plant type; it occurs on late tillers in summer and on volunteer crops in autumn, but it is most conspicuous in spring.

34.2 A detailed study of focus development

A more detailed study of focus development has been carried out with the help of an artificially established focus. In a small plot of Heines VII winter

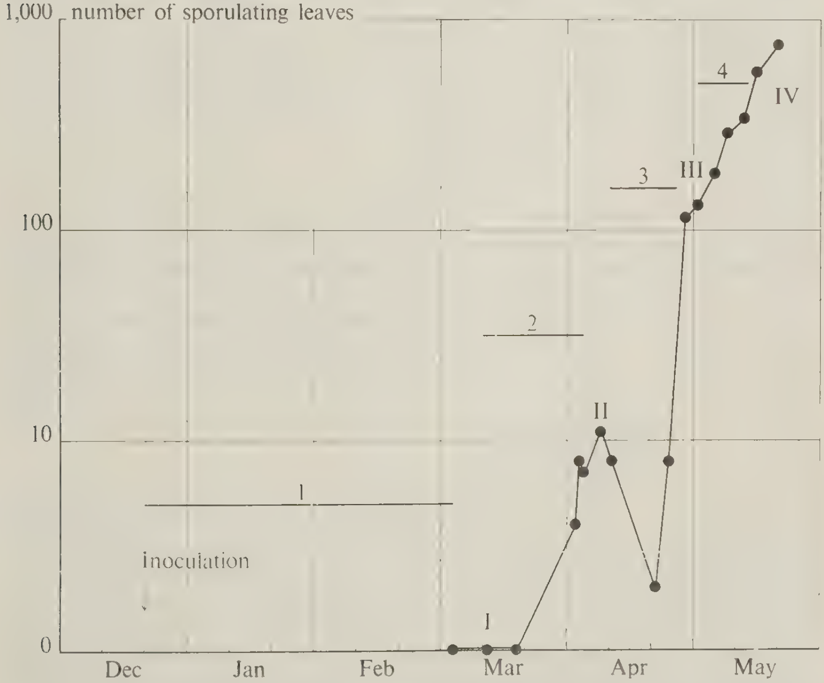


FIG. 34.2 A detailed study of focus development, 1958–59. The focus was started by inoculation of a Heines VII plot with race W 12. The number of leaves, counted at irregular intervals in a square measuring 1.5 × 1.5 m., has been plotted on a logarithmic scale. The incubation times are indicated by arabic figures, their length is given by the horizontal lines. The sporulation waves are indicated by roman figures.

wheat, sown on 30-10-1958, a focus of race W12 was established; the inoculation took place on 20–12–1958 at a GS = 1.1.3. The subsequent development was followed by counting at irregular times the number of sporulating leaves on a square measuring 1.5 × 1.5 m., the inoculated plants being at the centre of the plot.

The results are represented in fig. 34.2. Four sporulation waves can be seen (roman figures), preceded by four incubation times of different length, in good agreement with 32.2. The wavelike development of early infections is a generally observed phenomenon. Later development of the infection is smoothed because of the overlapping of incubation periods, the overlapping being the consequence of the random variation in the incubation times of individual leaves (32.3) and of the long duration of the sporulation time (in this period up to some weeks). The overlapping effect makes it already difficult to distinguish between the third and the fourth sporulation wave.

In the shooting period new leaves appear in rapid succession; the time interval between the appearance of two successive leaf layers is sometimes shorter than the incubation time of the rust. Thus though the rust epidemic continues to develop undisturbed on the lower leaves, with the appearance of the upper leaf layers the impression is given that the epidemic is receding. However, when another incubation time has elapsed, the upper leaves sporulate in their turn, giving the effect of a resurgence of the epidemic. Here the sporulation waves are not caused by the wave-like appearance of the inoculum but by the wave-like appearance of the substrate. Many farmers have been misled by this effect, because they did not go into their fields to see what was underneath the apparently healthy canopy of fresh leaves.

34.3 Wider implications of focal infection

Infection does not always take place when inoculum is present. Ecological conditions for infection may be favourable, unfavourable or marginal. Striking illustrations of marginal conditions are sometimes found, as in the case of wind shades. A colour slide made by Zijdewind during the epidemic of the year 1955, is good evidence: the field was clearly rusted in the wind shade area of a house, the rusted patch tapering out gradually. Probably here the crop dried more slowly than in the rest of the field so that infection could be established. Such phenomena are temporary, they may last one to three weeks and are then dissolved in the general epidemic.

Once the writer's attention was drawn to the fact that, according to the local observers, the yellow rust "came out of the house". The house in question had been taken down eight years before and no stone remained. What remained over from the house and its garden was a different chemical and physical composition of the soil. Though there was no visible difference between the wheat in the former garden and the rest of the field a minor microclimatic difference must have been present, due to minor differences in the development of the wheat as a result of the nutritional differences of the soil. By chance, the first focus developed in the former garden and when the rust spread the infection stopped within the borders of this area, so that a yellow "garden" was visible from the road. The phenomenon, which remained one or two weeks, must have been striking to the onlooker. When the writer was called the rust had already spread and the phenomenon was hardly visible.

On another occasion the writer was warned that somebody had definitely proved that the rust "came from the potatoes". The potatoes in question had been stored in a clamp on the border of the field two years before. We must assume that a focus developed accidentally in the wheat field on the place of the old clamp; certainly that crop was different from the rest of the field, as a result of nutritional differences after the soil had been disturbed by the digging of the potato pit and by the introduction of a large amount of straw. For some time the rust must have been limited to the site of the old clamp, due to minor differences in microclimate conditions, these being just favourable at that spot. When the writer saw the field the whole of it was severely infected, but the location of the potato clamp was still visible.

In trial fields it may also happen that one plot is conspicuously infected whilst other plots are free or show only beginning infection. Here again, a focus has developed in one special plot and for some time remained confined to that plot, due to the marginal infection conditions. Erroneously, this phenomenon has been used sometimes to demonstrate the capacity of the variety to carry over yellow rust with the seeds.

The Flamingo race is known to have overwintered the winter of 1958–1959 in the Noordoostpolder in one corner of field 9168. In this field yellow rust developed normally but the DA showed a gradient from the overwintering corner down to the other side of the field. The gradient remained up to harvest time. The spring was exceedingly dry and certainly the ecological conditions were marginal. The fact that the yellow rust could develop up to a DA = 10 has to be ascribed to the large amount of inoculum present on the spot from the winter onwards. At the other end of the field, where the ecological conditions were not visibly different, the amount of inoculum was not sufficient for the rust to reach a final DA = 10 during the marginal infection conditions. Surrounding fields of Flamingo, where the inoculum arrived later and in smaller amounts, were infected to a much lower DA; in the rest of the polder Flamingo was nearly free from yellow rust. The case of the Flamingo race is a particularly clear one, but many similar examples could be cited.

Flamingo / Noordoostpolder/9168/	6–1–1959/	2.1.3/4	/ 1	F 0	
	1–4	/ 3	/4 / 2	F 4	
	13–5	/ 7	/2–4/ 7→5		
	28–5	/10	/4 / 8→6		
	15–6	/10.53	/3 /10→8		
	17–7	/11.2	/– / †		E 2

On 1–4 there were about 30 foci of c. 5 leaves each.

In 1959 it was quite frequent that one field was severely attacked while surrounding fields of the same variety were practically free from rust. This phenomenon is also known from the literature and it has been puzzling the observers. We may make a generalization about the observations recorded in the foregoing and conclude that in such cases the weather conditions were marginal and that the rust developed only in these fields where it had been present from the winter onwards. In 1957 such a situation occurred in England: the spring was very dry and yellow rust was rather rare. Nevertheless a few heavily infected fields have been found by the writer.

In the hill country differences in exposure to wind and sun may help to create

the phenomenon of the isolated severely infected fields. Examples from Germany have been reported to the writer by Lein, but the writer has not seen such examples himself.

In mountain districts, neighbouring valleys may show quite different degrees of infection. This was seen during one of the writer's tours through Switzerland in the company of Dr. Kobel. The shallow Gürbe valley (canton Bern) runs parallel with the Aare valley at 4 km. distance and is separated from it by a ridge a good 100 m. above the level of the valleys. In the Aare valley yellow rust on the Probus fields could be seen during the drive without stopping the car, which implies a DA $\geqslant 8$; in the Gürbe valley the average was DA $= 4$. We may assume that yellow rust inoculum overwintered in the Aare valley and that the air masses carrying inoculum travel up and down the valleys, but do not easily cross the ridges.

The examples of the wind shade and of the rust which "came out of the house" or "from the potatoes" indicate that minor differences in microclimate can cause large, though sometimes temporary, differences in infection under marginal weather conditions; "marginal", whatever this implies physically, indicating such conditions that minor climatic differences determine success or failure of infection. An early and well established focus must be present before the weather conditions become marginal, as is illustrated by the Flamingo example where a gradient of infection indicated the original site of the focus throughout the growing season. Whether the focus becomes established "in the house", "in the potatoes" or in a particular corner of the field is, of course, merely a matter of chance.

The combination of three factors, relative scarcity of overwintering inoculum, hardly visible microclimatic differences, and marginal weather conditions, explains many oddities in the distribution of yellow rust in years without severe epidemic.

34.4 Focal and general epidemics

There are two extreme types of epidemics: the focal and the general epidemic. Most epidemics, however, are intermediate; they will start as focal epidemics and will generalize more and more as long as the weather is favourable. The focal or general origin of an epidemic is merely a matter of the amount of inoculum, either overwintering or wind-borne.

The epidemic in Southern Spain and Portugal which the writer saw in April 1958 (Zadoks, 1960) was a light focal epidemic, probably wind borne, which did not generalize. The rust remained restricted to a few foci. The 1956 epidemic in the Netherlands was a typical focal epidemic. Foci were observed from May onwards and remained visible until late in the growing season. The attack became generalized only in a few districts as in Zeeland and in Friesland.

During a general epidemic foci are not conspicuous. The Heines VII epidemic in the Netherlands in 1957 was a typical general epidemic without focal stage. In this year the general Heines VII epidemic contrasted clearly with the focal Alba epidemic. The marked difference led to the hypothesis of the existence of a separate Alba race, an hypothesis later proved with the help of the race nurseries (24.42, 24.52).

The origin of the difference between focal and general epidemics is clear. The

primary difference is the amount of inoculum with which the epidemic starts. The Heines VII epidemic in 1957 started with large amounts of inoculum, which overwintered on nearly every wheat field in the Netherlands. The Alba epidemic started with a wind borne inoculum, coming from a rather limited zone in Belgium and transported over fairly large distances. The amount of wind borne inoculum entering Holland was necessarily small.

34.5 Nutritional effects on host and parasite

Nutritional effects can be studied easily in fertilizer experiments which are conducted on every experimental farm in the Netherlands. When the wheat growth is too poor to give a good yield the rust does not grow well; IT and DA will be low. When the wheat is normal the rust development is normal too. When the wheat growth is too lush the rust develops with high IT but relatively low DA, probably because of a decreased accessibility of the crop to the inoculum. Rust develops intensely at the trial borders, as there the wheat growth is rich due to a surplus of nutrients and because there the crop is easily accessible to the inoculum. On the whole, the range of nutritional conditions over which the rust develops normally is rather wide.

To large scale epidemiology nutritional effects are of little importance, because the variations in the nutritional conditions of the normal farmer's crop is well within the tolerance range of the yellow rust. Allowance has only to be made for those instances, where small nutritional differences lead to minor variations in the development of the crops and of their microclimates, variations which are sometimes revealed by temporary differences in the intensity of the rust infection (34.3).

34.6 Centres of rust development

In the foregoing pages it has been shown that in the Netherlands yellow rust is endemic. The Netherlands, together with Belgian Flanders, form an endemic centre from which rust may spread to neighbouring countries, where the rust races meet suitable carrier varieties. Owing to its nature the highly specialized Alba race cannot emigrate, as its carrier variety Alba is not cultivated outside the afore mentioned region. Neither can it have immigrated from another region. This race is "made in Benelux". For this and other races the Netherlands and their adjoining regions are certainly a centre of propagation.

In Switzerland Kobel has shown that yellow rust is endemic in the same way as it is in the Netherlands. The only race seen on the yellow rust trials is the Probus race, which can certainly not emigrate since it does not attack the usual commercial varieties; for the same reasons it could not have immigrated. The Probus race must be a "product of Switzerland". For this race Switzerland is a permanent centre of development.

In the months March and April when the Dutch and Swiss epidemics start to build up, another centre is present in Southern Spain and Portugal, with a possible outpost in the Montpellier region. We are still badly informed on the race(s) present. Field observations suggest wind-borne inoculum, that may have come from Morocco (Zadoks, 1960). When the Iberian season remains cool and moist, the rust may develop into a locally serious epidemic, as in Portugal 1959 and 1960 (Santiago).

At least three centres of yellow rust can be distinguished in Western Europe

with simultaneous development of the epidemic, map 34.5. Their simultaneous occurrence rules out the possibility that the epidemic in any centre is started with the inoculum from another centre. The independance of the Swiss centre is guaranteed by the character of the Probus race. The independance of the Dutch centre is confirmed by the winter observations and by considerations on race-variety compatibility.

The Dutch and Swiss endemics of yellow rust are clearly evident. The question arises as to whether the endemics are a consequence of climatic conditions or not, since the climate in the Netherlands and in the Swiss lowlands have several characteristics in common. Without a suitable climate there will be no endemics, nor will there be endemics without a compatible variety-race combination. Still, climate and compatibility are linked, the link being the degree of compatibility expressed in the quantity CI. A CI of 40 to 50 (Probus in Switzerland and Heines VII, Alba and Triumph in the Netherlands) in combination with the climate of these countries is sufficient for a race to be endemic with a constant threat of severe epidemics. When, however, Michigan Amber with a CI = c. 100 had been grown over large parts of North-west Europe, the rust should have been epidemic in all countries independent of local climates.

These considerations lead to two concepts: first that an endemic varies in degree from locality to locality, second that an endemic is variable in time. The variability in degree from locality to locality is demonstrated by the fact that in Switzerland and in the Netherlands there are relatively important epidemics every year, whereas in France and Belgium the epidemics are milder; in England and Denmark they are usually innocuous. Nevertheless, yellow rust in France, England and Denmark must be endemic, because infection from Switzerland and the Netherlands is usually impossible due to the incompatibility of the migrating race with the invaded varieties.

Variations in the intensity of epidemics in time are a logical consequence of the continuous changes of varieties and cultural methods. A susceptible variety is replaced by a resistant variety; correspondingly, the intensity of the endemic decreases from a high to a low level.

All this indicates the variety as being the determinant factor causing a high intensity of the endemic. Another point has to be made: a favourable climate is a constant invitation for new races to try their luck, but the building up of a severe epidemic from the first pustule of the new race onwards takes at least one complete year and probably even two successive years. A third requisite for a high intensity of the endemic is an intensive cropping of the carrier variety.

35 OVERSUMMERING OF YELLOW RUST

35.1 Availability of inoculum in the dying crop

Leaves which die off far enough to show chlorophyll only here and there around a relatively young lesion (island effect) can still sporulate abundantly under favourable conditions. During a very hot spell in June 1957, a trial field was visited in the early afternoon; the leaves of Heines VII plants, though still somewhat turgescent, apparently died from yellow rust.

When late in the afternoon a thunderstorm approached, the writer went out to see the wheat again. He was astonished to see the "dead" leaves sporulating heavily. Counts revealed an average of 2×10^6 spores per leaf. Dead or nearly

dead leaves apparently may produce spores as long as they remain turgescent. Such leaves are certainly present in the crop until a few days before harvest.

35.2 Oversummering on wheat under Dutch conditions

When the crop ripens the leaves die and with them dies the yellow rust mycelium. However, some leaves remain green longer than others. These are the leaves of plants growing on a spot with more moisture or nitrogen in the soil, e.g. the field border, a low lying part of the field, a small patch where the sowing machine failed, or the filling place of the fertilizer machine. Mostly the leaves belong to late tillers. They do not fail to show some yellow rust lesions when the crop is heavily infected.

When the crop is harvested some of these late tillers may be spared, still carrying their spore loads into the wind. The volunteer crop will be infected immediately after its emergence. Pre-harvest late tillers, spared by the cutting knife and showing yellow rust lesions are very rare and number not more than 1 per 10 m. field border length.

The same plants, which may have late tillers, may also have young sprouts which escape the attention of the observer. When the not yet fully ripened plants are cut, the still active roots force the sprouts to shoot. In the diseased crop the sprouts can hardly escape infection but at harvest time this infection cannot yet be seen. A week after harvest time the sprout is a post-harvest late tiller which can show one or two yellow rust lesions. As the shortest possible incubation time in the summer is c. 11 days, the infection must have taken place before the harvest. Post-harvest late tillers showing yellow rust are relatively frequent, but seldom more than 1 per 100 sq.m.

Pre-harvest volunteers occur in clusters, as described in 12.13. At the day of harvesting their leaves are 1 to 3 cm. long. These can hardly escape infection in a diseased crop. About a week after harvest the first lesions on such clusters can be found. Again, as the shortest possible incubation time is 11 days, the infection must have taken place before harvest.

There is often some wheat standing about in odd places, usually in aberrant growth stages. Sowing time experiments of breeders belong to this category. Near the barn where the chickens feed one can be sure to find some wheat plants, near the manure heap and the threshing place, in the garden or on the road side, or in the potato crop. All these wheat plants, wherever they come from, belong to the category of adventive plants. They have one characteristic in common: a lower growth stage than the normal crop. When they carry yellow rust, as they occasionally do, they are not cut off by the harvester nor do they die, as it is not yet their time. So they can carry over the inoculum from the normal crop to the volunteer crop. In yellow rust of wheat this sequence is rare, in yellow rust of barley, however, it is quite frequent.

A special type of adventive wheat originates when part of a field is cut for the purpose of building a new farm or digging a new ditch. The cut, wheat sprouts again and ripens one month later than the original crop. In that month, August, it may be well infected with yellow rust. This way of oversummering is not infrequent in the reclamation area where new farms are constantly being built.

During harvesting many grains are shed, up to 1,000 per sq.m. or more; these grains germinate to give a post-harvest volunteer crop which receives the in-

oculum from any source, be it pre- or post-harvest late tillers, pre-harvest volunteers or adventive wheat. When the farmer comes to plough or to cultivate he destroys numbers of self sown plants, but many remain and it happens rarely that the farmer succeeds in burying all rust infected volunteers. So the yellow rust thrives on the volunteer crop and oversummers there to infect the autumn sown crop in late autumn and, eventually, the rust overwinters on the volunteers to infect the winter wheat in spring, as even the autumnal deep ploughing will not eradicate all volunteers.

In those cases where grasses or clovers are sown under cover of the wheat and there is no ploughing, enormous amounts of inoculum may survive until next spring. A bad crop of clover gives a good crop of wheat and of yellow rust. Such clover fields and also seed grass crops have been observed to infect the whole neighbourhood. Since Yellow Trefoil is ploughed under in late autumn and a good crop of Yellow Trefoil does not allow the volunteer plants much room in which to grow, Yellow Trefoil is the most innocuous of the clover crops.

Every now and then a farmer is so pleased with his volunteer crop, that he maintains it as an early sown production crop. These are among the most dangerous of the sources of inoculum. At the onset of the 1955 epidemic ZIJLSTRA in Friesland found a large amount of yellow rust on such a crop. In 1958 a similar case was encountered in the Haarlemmermeerpolder; the wheat was considerably infected with yellow rust: Heines VII / Haarlemmermeerpolder 8067/14–2/V4.1.3/4/3.

Oversummering of the rust in the form of uredospores is hardly feasible, because yellow rust spores rapidly loose their vitality in an atmosphere of high humidity (at night) and of high temperature (BECKER, 1928). Also as the writer has experienced, spores are easily washed from the leaves by rain.

35.3 Oversummering at high altitudes

In the Alps there is a possibility of oversummering which is not available in the low countries. Wheat is grown at altitudes up to 1,200 m. At these altitudes harvest is late, sometimes even in September. As these fields are sometimes heavily rusted the yellow rust can oversummer here. From these high refuges, the wind may carry the inoculum down to the volunteer crop in the valleys.

The upward transport of inoculum is proved by the infection of trials sown by the *Eidgenössische Landwirtschaftliche Versuchsanstalt* at high altitudes in valleys where no wheat is grown. The most remarkable trial was at Maran near Arosa at a height of c. 2,000 m. The nearest wheat fields were in the Rhine valley near Chur at a height of c. 600 m. and at a radial distance of 13 km. from Maran. In 1959 these fields showed a focal attack of light intensity, DA = 0 to 4F6, when visited on 26-6-1959. KOBEL (1959) found the first infection at Maran at the end of July.

Downward transport cannot be proved so easily. Therefore the existence of a high altitude infection cycle in the Alps is not proved, but it is quite plausible. In the Himalayan foothills a high altitude infection cycle was demonstrated convincingly by MEHTA (1940, 1952).

35.4 Oversummering on secondary hosts

Grasses might act as secondary hosts. The problem has been discussed ex-

tensively in 22. Oversummering on *Agropyrum* species seems to be possible in rare cases. They are rare indeed, as only a few positive data are available over a period of 60 years of yellow rust research. As far as the writer's personal experience goes, the amount of inoculum on secondary hosts is so very small compared to the amount of oversummering inoculum on the wheat itself, that it is of no consequence to the epidemiology of yellow rust on wheat.

36 SPORE DISPERSAL

For the purpose of this discussion, three categories of spore dispersal may be arbitrarily distinguished: short distance dispersal measured in decameters, medium distance dispersal measured in kilometers, and long distance dispersal measured in hundreds of kilometers. Mechanized spore traps could not be used in dispersal studies, because it is too difficult to distinguish the uredospores of yellow rust from those of other graminicolous leaf rusts in routine work. The International Yellow Rust Trials were quite useful as living spore traps.

36.1 Short distance spore dispersal

It is amazing to observe how, at times, even very small distances cannot be bridged by wind borne spores. When in the winter a natural or artificial focus is established in a drill, the focus will extend along the drill as a result of the wind rubbing the sporulating leaves with their spore load against the adjoining uninfected leaves; but it may take months before the neighbouring drills at 25 cm. distance are infected, when there is no bodily contact between sporulating and healthy leaves.

In marked contrast to the aforementioned observations are the observations reported hereunder. An explanation for this contrast should be sought in differences in the amount of inoculum and in infection conditions.

As in the Netherlands wheat never follows wheat, a single infected leaf in the middle of a wheat field indicates that spores have been carried over a distance of at least the distance between the sporulating leaf and the nearest field border. In this way it could easily and repeatedly be established that spore dispersal over distances up to c. 100 m. occurred regularly in autumn and in winter, in a period when inoculum was not abundant.

Similar observations on late tillers and volunteers in summer indicated dispersal distances up to c. 10 m.

36.2 Medium distance spore dispersal

It is most difficult to find out about spore dispersal over medium distances in a country where yellow rust is endemic. Two circumstances favoured spore dispersal studies, the first being the frequent occurrence of new races, the second being the great reclamation works in execution in the former Zuiderzee.

The Flamingo race has already been described (24.42; 24.52); in 1958 only one field in the Noordoostpolder was markedly infected. In this field the rust survived, not by grace of an especially favourable summer, but because of serious negligence of the farmer. The 1959 story has been told in 34.3: field inspection and other intelligence indicated that field 9168 was the main source, if not the only source, of inoculum of the Flamingo race in the polder. The perpetual drought of 1959 prevented a catastrophe, but in June some Flamingo

TABLE 36.2 Medium distance spore dispersal in Oostelijk Flevoland

trial		date of first observation	variety	GS	DA	distance to nearest wheat area in km.
Ketelhaven	3550	16–1	Persian	2	2	1.8
Lelystad	3560	1–7	Rubis	10.54	8	18.0
Knarhaven	3570	1–7	Harvest Queen	10.51	2	15.8

fields in the neighbourhood were sufficiently infected to justify the conclusion that the Flamingo race was spread over a distance of c. 9 km.

Clearer indications were found at the time, when the new polder Oostelijk Flevoland consisted only of a narrow strip of dyke in the midst of the waters. Yellow rust trials were established on this dyke with the kind permission of the Board of the Zuiderzee Works. The distances to the nearest wheat areas are given in table 36.2.

The data from Oostelijk Flevoland with dispersal distances of 1.8 to 18 km. are in accordance with the Swiss Maran experiment (35.3) with a minimum dispersal distance of 13 km. In Oostelijk Flevoland and at Maran the distance must have been covered in one single step. Care was taken that no inoculum reached the trials in Oostelijk Flevoland by means of the boots or clothes of the trial inspectors.

36.3 Long distance spore dispersal

In 1957 there was an epidemic on Alba caused by a new race, the Alba race (24.52). A few visits to Belgium showed that the centre of the epidemic was in the Flemish sea polders. In Zeeland there was a heavy focal infection, in the Wieringerwaard there was a light focal infection (map 36.3). Apparently the new race had travelled northwards along the coast, carried by the prevailing south-westerly winds over a distance of 200 km.

In the Netherlands there was a severe epidemic on Heines VII in 1955, caused by the Heines VII race (race 7x, W 16). It is nearly sure that this race originated in the Netherlands (24.52); it is certain that the Netherlands were the main source of inoculum. The International Yellow Rust Trials and the race identifications at Braunschweig showed, that the race has spread over large parts of North-west Europe (map 36.3), covering distances up to 800 km. Whether the inoculum spread during the epidemics of 1956 and 1957 or during the epidemic of 1955 (with subsequent oversummering and overwintering at the new habitat) cannot be said with certainty; the writer is in favour of the second possibility.

The writer's observations in Spain and the data communicated to him by SALAZAR and VILLENA suggest a yearly recurring gradient of severity and of the date of first observation from the south to the north. Though other explanations can be put forward, the most plausible explanation is that the gradient is a gradient of transport, inoculum coming from some southern source (ZADOKS, 1960). If this explanation is true, the rust travelled considerable distances, the distance from the Spanish south coast to Zaragoza being c. 600 km.

In none of the foregoing examples can it be ascertained whether the distances were covered in one or in several successive steps, with intermediate establishment and multiplication of inoculum. ZOGG (1949) demonstrated a direct re-

lation between the distance of spore dispersal and the dimension of the focus; consequently the writer presumes one step dispersal, at least in the case of the Heines VII and Alba races.

In the U.S.A. yellow rust is not endemic, except in the northern states west of the Rocky Mountains where it is of minor importance. In 1957, and still more in 1958, yellow rust appeared in a narrow band over the whole breadth of the States. The source of the inoculum was in northern Mexico, a rather severe epidemic was established in northern Texas, localized epidemics and foci were found in many states up to Langdon in North Dakota, 20 miles south of the Canadian border (BRIDGMON & KOLP; FUTRELL a.o.; GOUGH a.o.; HENNEN & KOMANETSKY; MILLER & CHRISTENSEN; PADY & JOHNSTON; ROSEN a.o.; 1959). No yellow rust was found in neighbouring Manitoba, Canada. In map 36.3 the map of America is superimposed over the map of Europe, both maps being on the same scale. The dates of the first observation and the probable dates of first in fection have been noted for every state. The rust covered c. 2,400 km., a distance from North Africa to Norway. In view of the observation dates and the observed severities of infection, it is certain that the rust covered the distance in several steps and needed a period of something short of a half year for the whole trip.

The American data are matched only by those of MEHTA (1940, 1952), who in the course of his admirable rust studies in India drew wind trajectories of spore clouds covering up to 1,000 km. Here the evidence is in favour of a one step transport over the whole distance.

It must be emphasized that long distance spore dispersal of yellow rust, in one step as well as in several successive steps, has been established only in the U.S.A. and in India, but in Europe the evidence is still circumstantial. Long distance spore dispersal of stem rust in Europe has been demonstrated by OGILVIE & THORPE (1958) for a trajectory from the Iberian Peninsula to England, covering c. 1,500 km.

36.4 The establishment of races

As it is sure that long distance dispersal can take place, it has to be ascertained whether this dispersal is a real danger to the European wheat culture and the Dutch wheat culture in particular.

In view of the extreme specialization of yellow rust this danger is usually small. The political situation in Europe with its many national frontiers led to a good many national or semi-national varieties; a development enhanced by the great climatic variation present in Europe. The Dutch Staring, the English Hybrid 46 and the Swiss Probus are examples of national varieties. As the national varieties usually differ in their genetic composition of resistance, the suggestion of JOHNSON (1958) to organize a regional distribution of resistance genes has already been put in practice.

Only few varieties have such outstanding qualities that they are cultivated over large areas (map 36.4); these are e.g. the French varieties Nord and Cappelle and the German variety Heines VII. In their train followed the Cappelle, the Heines VII and the Peko race (races B 2x/55, B 7x and B 54; map 36.4); a good demonstration of the validity of JOHNSON's ideas.

The answer to the question of the first paragraph is that varieties, however good they are, should be restricted to a relatively small area; this restriction reduces, but does not eliminate, the danger of local rust epidemics.

The history of the epidemics studied (24.52; table A.24.51) does not suggest that severe epidemics have been caused by wind-borne inoculum transported over great distances, as was the case in the U.S.A., 1958 (36.3). The evidence indicates that the races were already present and took advantage of favourable weather combined with a large acreage of the carrier variety; eventual long distance dispersal and subsequent establishment must have taken place in a year previous to the epidemic. Another possibility is that a new race originated on the spot by mutation or recombination.

After its initial appearance, a race has to establish itself in its new home. Theoretically only one wheat plant is needed. Few observations are available on this point. In the two polders "Wieringerwaard" and "Waard- en Groetpolder" Alba was grown to some extent in 1957. Some fields were moderately infected. The rust overwintered on volunteers in a few corners of these Alba fields. In 1958 the only two Alba fields known to the writer showed a focal infection, suggesting that the Alba race established itself in an isolated region on a few fields, lying within a radius of 10 km. The establishment of the Flamingo race (34,3) needed only c. 100 sq.m.

37 WEATHER TYPES AND THE DEVELOPMENT OF YELLOW RUST

37.1 The sporulation time

The sporulation time is the time in days during which a leaf sporulates. The sporulation time has received little attention in epidemiologic studies; it is difficult to make assessments of sporulation times of individual leaves.

The maximum possible sporulation time is the maximum lifetime of a leaf minus the incubation time. This maximum, however, is never attained, because the sporulating leaf is vulnerable to adverse conditions. In practice, sporulation times vary from a few days to a few weeks. The sporulation time may be discontinuous, when the sporulating part of the leaf is killed and the infected but non-sporulating part is spared (33).

37.2 Weather types and the rust

The influence of individual microclimate factors on yellow rust in the field has not been studied, with the exception of the relation between average temperature and incubation time (32.2). Out of his personal experience the writer will try to describe some weather types, which have a definite influence on the development of the rust.

Low temperatures in the winter, possibly combined with little solar irradiation, cause prolonged incubation times (32.2) and decreased infection results (32.4). At an average day temperature of c. 5°C. yellow rust still sporulates well. It is probable that sporulation and infection come to a stop at temperatures near 0°C. During mild frosts the temperature at 10 cm. height may be so low that the sporulating parts of the leave are killed, thereby shortening the sporulation time of the leaf. At still lower temperatures the mycelium in the non-sporulating leaves may suffer (GASSNER & PIESCHEL, 1934). During a rigourous winter wheat and rust may be winter killed. The ill-effects of a severe winter are insufficiently counter-balanced by a long incubation time and the amount of rust decreases, but during mild winters, as in the winter of 1956–1957, the amount of rust increases slowly but steadily.

In late winter, a weather type is sometimes prevalent in which snow and rain, freezing and thawing alternate in rapid succession. This was actually the case in March 1958; during that month the amount of rust decreased visibly in some fields due to a lack of propagation possibilities. The oldest leaves, having lost their cold resistance, die quickly in this weather and with them dies the rust, which at that time is still concentrated in the lower leaves. Sporulation times are necessarily short when this weather type prevails. Leaves contacting the soil because of the impact of rain or the loss of turgescence are poor subjects to propagate yellow rust; they are soon covered by dirt and rot away.

In the Netherlands, there is usually a period of about four weeks in early spring when dry and cold easterly or north-easterly winds blow incessantly. At night there is little or no dew. In this period the rust may sporulate nicely, but few infections result because of the lack of humidity. The rust develops only where a large amount of inoculum was already present before the onset of the drought and typical focus phenomena come into being. This type of weather does not appreciably infect the sporulation time.

Abundant rains can be expected in May, when the winter wheat has a GS = c. 6. High humidity is favourable to sporulation and infection alike, but the rains wash the spores from the leaves and out of the air. Heavy rains may bend the lower leaves to the soil and cover them with dirt, thus abruptly ending the sporulation time. In one instance the writer saw a decrease from PA = 5 to PA = 1 within three days. McKay (1957) states that in Ireland, where the rainfall is greater than in the Netherlands, the dry years are yellow rust years.

Heat usually decreases the compatibility, without really killing the rust. A hot spell in mid-June, 1957 effectively stopped the increase of the epidemic, thus preventing severe losses. Drought, especially continued drought as in the spring and summer of 1959, reduces the number of new infections and probably also restrains the sporulation. Progress of the epidemic is only possible when large amounts of inoculum were present before the onset of the drought.

Infection is not always impeded by drought, as was observed during the very dry summer of 1959. In a Heines VII plot on the Wageningen trial grounds yellow rust oversummered in the usual way, passing from late tillers to volunteers and even forming foci in the months July, August and September. Dew was recorded nearly every night with a De Wit leaf wetness recorder; apparently this dew was sufficient to permit the propagation and dispersal of the rust.

37.3 Weather types and the host

During the last few years there was a marked relation between a wet summer in the one year and a severe epidemic in the following year. This relation could not be explained by a rust-weather relation, as is well demonstrated by the example in the last paragraph of 37.2. To know more about the rust it is necessary to study also the host-weather relation.

In the dry summer of 1959 the crops ripened evenly and they were harvested without delay; loss through shedding of the grains was at a minimum. For these reasons the amount of late tillers and volunteer wheat was very low. On the unploughed fields, the grains lay ungerminated until well into September. On those fields which could be tilled, few host plants remained. The possibilities of survival of the rust were restricted to a minimum because of the lack of a suitable substrate.

Of the wet summers 1954, 1956, 1957 and 1960 the last was the worst. Because of the continuous rainfall, the wheat seldom dried sufficiently to be harvested; also, the soil was so soaked that it could not support the harvesting machinery. Due to the great delay in harvesting, many heads fell on to the earth and there sprouted; many grains were shed and germinated immediately. Plenty of late tillers were present. As there was such an enormous amount of substrate, yellow rust oversummered abundantly. Because of the soaked fields, which could be ploughed only late in the autumn, the rust developed freely during the summer and early autumn. The events in the summer 1954 have not been followed, those in 1956 and 1957 showed a resemblance to the events of 1960.

These few, but extreme, examples are adequate to demonstrate the importance of the summer weather in the epidemic cycle of yellow rust, a preceding wet summer being a requisite for a severe epidemic. The effect of the summer weather is not due to a rust-weather but to a host-weather relation.

38 DISCUSSION

ERIKSSON & HENNING (1896) already knew the main points of the life cycle of yellow rust. They observed the overwintering of the rust, and from their data incubation times of c. 150 days (under snow cover) can be calculated. They did not fully appreciate the significance of their own findings, being firmly in the grip of the mycoplasma theory (ERIKSSON, 1910). HECKE (1915) saw a direct relation between overwintering and severe outbreaks of yellow rust. From his data an incubation time of c. 100 days may be calculated. Other scientists reported on the maximum incubation time observed, a.o. HUNGERFORD (1923b) 30 days and MEHTA (1923) 36 days.

Overwintering of yellow rust on wheat has been observed by many people in many countries, e.g.

Austria	– HECKE (1915)
Denmark	– NIELSEN (1875 ex ERIKSSON & HENNING, 1896)
England	– BATTS (1957b), BIFFEN (1908), BROOKS (1944), MEHTA (1923)
France	– BLARINGHEM (1914), DUCOMET & FOEX (1925), VIENNOT-BOURGIN (1934)
Germany	– BECKER & HART (1939), BONNE (1928), GASSNER & PIESCHEL (1934), LANG (1918)
Ireland	– MCKAY (1957)
Netherlands	– this publication
Sweden	– ERIKSSON & HENNING (1896)
U.S.A.	– HUNGERFORD (1923b)

Some of these authors mentioned yellow rust on volunteer wheat, i.a. BIFFEN, DUCOMET & FOEX, HUMPHREY a.o. (1924) and MEHTA; JOSHI (1957) mentions ratoon tillers (= post harvest late tillers) as a substrate. Overwintering on grasses is recorded by ANONYMOUS (1917), BECKER & HART (1939), HUMPHREY a.o. (1924), VIENNOT-BOURGIN (1934, 1939) and the writer (22.2). In April 1846 TREVIRANUS (1846) saw yellow rust of rye only on the lowest leaves, formed before the winter; a very severe epidemic followed.

Oversummering of yellow rust of wheat on grasses was observed by HUMPHREY a.o. (1924) and BECKER & HART (1939) (see also 22). Oversummering on

late tillers and volunteer wheat was found by BECKER & HART (1939), BRIDGMON & KOLP (1959), ERIKSSON & HENNING (1896), HUMPHREY a.o., OVERLAET (1958b; artificial infection) and the present writer.

The idea of the oversummering of yellow rust in the seed has been introduced by ERIKSSON's mycoplasma theory (1910) and has never completely died since. Superficial indications for oversummering in the seeds derived from variety trials are easily explained by the theory of focus formation. Substantial proof of the oversummering in seeds has never been produced; negative evidence was given by MEHTA (1923). HUNGERFORD (1923b) did all that was possible to prove that the seeds did not carry over rust inoculum from one season to the other.

Focus formation has received little attention in the literature. GASSNER & PIESCHEL (1934) did a few measurements. As a typical phenomenon, foci have been mentioned by DROOGENDIJK (1937), KOBEL (1959) and PADY & JOHNSON (1959).

Infection conditions have been studied in the laboratory by STRAIB (1940). Free water is necessary for germination; the temperature range for germination is wide, with a relatively low optimum temperature.

A difference of 12 °C. during the multiplication of the inoculum results in a difference of c. 3 °C. in its temperature optimum for germination. Many authors are at variance about the exact value of the temperature optimum for germination, which can be probably put at c. 12 °C. (NEWTON & JOHNSON, 1936; STRAIB, 1940; WILHELM, 1931).

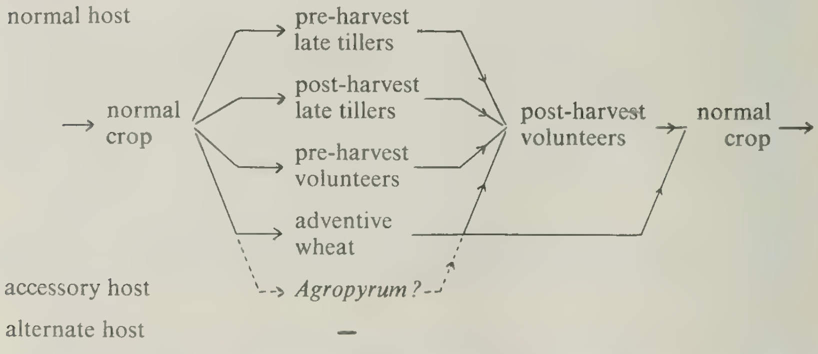
Extensive studies on spore viability have been made by BECKER (1928). She showed that viability decreases rapidly with increasing humidity and temperature of the air; yellow rust spores are much more sensitive to adverse environmental conditions than brown rust or black rust spores. These results are very important for the epidemiology. The viability of yellow rust spores is such that a good percentage of them will be alive after one or two days of long distance transport in the upper air; at the same time the viability is so low that oversummering and overwintering of yellow rust as spores is not possible in a humid and mild climate.

An analysis of the weather types favourable to the development of yellow rust has been attempted by several writers, but many of the earlier attempts were misdirected. HECKE (1915) and HUMPHREY a.o. (1924) saw the importance of a heavy autumn infection; BEAUVERIE (1923), HECKE (1915) and TREVIRANUS (1846) mentioned a mild winter as a rust favouring factor. BECKER & HART (1939) suggested that the summer coolness of the mountain valleys provided a good summer refuge for the rust. OVERLAET (1958b) found that the moist maritime climate of the Belgian coastal area was very favourable to yellow rust development. The difference in yellow rust development between the moist valleys and the dryer hills has been observed by several authors, among these being MÜLLER & MOLZ (1917).

39 CONCLUSIONS

It is not yet possible to give an overall view of the conditions leading to a severe epidemic. However, it is clear that a variety of factors must severally approach the optimum to result in a severe epidemic.

Schematically the epidemic cycle of yellow rust in the Netherlands is the following:



Prerequisites to an epidemic are the presence of a carrier variety and a compatible race. The race must be present approximately one year before the epidemic reaches maximum intensity; it may have immigrated by air travelling a long distance or it may have originated on the spot. The rust has only a limited number of generations at its disposal, at the most c. 17 a year.

From July until April the rust has to contend with enormous losses. These can be counteracted only when in the summer (the danger period) the farmers cannot keep the rust in check by destroying an adequate amount of substrtae because of heavy rainfall. The special conditions favouring the development of the rust should continue until the new autumn sown crop emerges.

From then onwards to the top of the epidemic the rust has at most c. 9 generations at its disposal. A severe epidemic follows only when the winter is so mild that the rust develops continuously; a difference of a few centigrades in the average temperature makes a difference of many generations. A general epidemic cannot develop when the acreage of the carrier is too small.

The acreage factor starts being important in the season preceding the epidemic. It is not so much the acreage itself which is important as the relative density of the carrier cultivation, expressed in percentages of the land area. The higher this density in the year preceding the epidemic, the more oversummering infection centres are present to infect the new sown crops in autumn. The number of infection centres, as well as the relatively short distances between these centres and the fields to be infected, contribute to the effect of the density of the carrier cultivation. These short distances enable the rust to infect the fresh crops at an early date, when the amount of inoculum in the infection centres is still low.

Focus phenomena appear when any of the factors mentioned above is suboptimal.

None of the factors mentioned in this chapter is exclusively responsible for an epidemic. This is demonstrated by the data of table 39 in which some of the major points have been summarized. The large acreages of 1956 and 1957, the wet summer of 1956 and the mild winter of 1957 attribute to the early epidemic of 1957. The later but severe epidemic of 1955 can be attributed in part to the

large acreages of 1954 and 1955 and the wet summer of 1954, but the amount of inoculum at the end of the growing season 1954 was probably a limiting factor. That 1956 did not bring an epidemic, though the acreages were big enough, can be ascribed to the dry summer of 1955 and the cold winter of 1956. In 1958 there was no severe epidemic; it is presumed that the acreage became one of the limiting factors, most of the Heines VII acreage being outside the coastal danger area. In 1959 and 1960 weather conditions and acreages were both limiting factors, and yellow rust on Heines VII nearly disappeared. The excessive rain in the summer of 1960 led to an unforeseen increase of inoculum in those few oversummering centres where yellow rust was present.

TABLE 39. Environmental conditions in the Netherlands in relation to the severity of the epidemics on Heines VII winter wheat

harvest year	1954	1955	1956	1957	1958	1959	1960	N_{30}
severity of the epidemic	s	E	F	E	F	s	s	.
acreage of Heines VII in ha.	33,000	28,000	14,000	15,000	6,000	4,000	7,000	.
N_g, De Bilt (1-8 until 31-7)	17.8	17.4	17.3	19.2	16.5	19.2	18.6	17.1
n_g, De Bilt (1-11 until 30-6)	9.2	8.3	8.3	10.4	8.0	9.7	9.5	8.3
rainfall in mm. July + Aug.	+100	–60	+111	+86	+21	–52	+124	156
rainy days July + August	+ 2	– 7	+ 9	+10	+ 4	– 7	+ 15	22

N_{30} = potential number of generations based on normals over 1921–1950 from the principal meteorological station at De Bilt.
s = yellow rust sporadic
E = severe epidemic
F = focal epidemic
rainfall expressed as excess to N_{30}
rainy days, number of days with more than 1 mm. rainfall, expressed as excess to N_{30}

4 QUANTITATIVE EPIDEMIOLOGY

This chapter relates to the quantitative aspects of yellow rust epidemiology. It is mainly an attempt to give an adequate graphical representation of the development of an epidemic, which is the result of the interaction between two populations, one of the host and one of the parasite. The study of population dynamics of fungus diseases is in its infancy. Therefore, and also because the writer is not qualified in mathematics, no theoretical aspects have been considered.

41 TERMINOLOGY

This chapter deals with host and parasite populations. Usually populations are build up of individuals, but in the case of wheat it is often difficult to distinguish individuals. Moreover in the case of rust it is questionable whether it is permissable to use the term "individuals".

Though a wheat crop is certainly built up of individual plants, the wheat plant is not the basic unit in population studies of this kind. The basic unit is the "leaf layer", a theoretical concept explained in 43.1 and illustrated in fig. 43.7. Essentially, the "leaf layer" consists of leaves of the same age. Only in the off-

season, the "wheat free" period, individual wheat plants become important items.

The rust population can be measured in many ways but rarely can be expressed in the number of "individuals". This is only possible when the infection level is so low, that "individual lesions" can be counted. To simplify the computations the area of a lesion on seedlings and on transition plants is arbitrarily fixed at 1 cm^2; the area of a lesion on a mature plant is fixed at 0.1 cm^2.

To express host and parasite in the same unit they are measured in projected living leaf area in the case of the host, in projected living and rusted leaf area in the case of the parasite. The "leaf mass" LM is the projected living leaf area (in square centimeters) of the wheat. The "rust mass" RM is the projected living and rusted leaf area (in square centimeters) of the wheat. LM and RM can be measured or estimated for any given object, be it plant, field or country.

For comparative work other units have been chosen. The "leaf mass index" LMI is the leaf mass in square centimeters per hectare. The "rust mass index" RMI is the rust mass in square centimeters per hectare. Whereas LM and RM must always be expressed in square centimeters, LMI and RMI are expressed in proportionate numbers. LMI is simply related to the "leaf area index" LAI of WATSON (1947a): LMI $= 10^8 \times$ LAI.

Several types of diagrams have been examined as to their use for the graphical representation of wheat and rust development. On the vertical axis representing wheat or rust several scales have been tried, a.o. the logarithmic or log scale and the logistic or logit scale. Along the horizontal axis, representing time, two time scales have been applied, the linear time scale and the i-time scale. Depending on the scales used, the diagrams are called:

log-linear diagram
logit-linear diagram
log-i diagram
logit-i diagram

42 THE LOGIT LINE

42.1 The percentage sigmoid

Usually rust is assessed as the percentage of the total leaf area which is covered by rust. When the successive percentages of one object are plotted against time, the resulting curve has a sigmoid shape. As an example, the observations from Harvest Queen 1958 in International Yellow Rust Trial 3460 are represented in fig. 42.1.

Sigmoid curves representing the growth of the rust population are difficult to draw and to interpret. The lower values (0,001 to 0,1 %), which are the more interesting ones, all come together in one class: 0.

Several other ways of representation are possible. In fig. 42.1 the same observations have been plotted on a percentage scale (PA), on a logarithmic scale (log PA) and on a logistic scale (logit $_{PA}$). All curves are drawn so that they have the 50 % value as a common point.

When plotted on a logistic scale the observations fit reasonably well to a straight line; on the percentage scale they fit equally well to the logistic curve

which is the transformed straight line of the logistic scale; on the logarithmic scale the observations fit to a straight line in the lower part of the scale only.

42.2 Choice and application of the logistic transformation

Sigmoid curves are not attractive for studies in population growth. A transformation to straight lines by one of the available mathematical methods is to be preferred. LARGE (1945, 1952) used the probit transformation in work on *Phytophthora*, VAN DER PLANK (1960) based an interesting theoretical approach on a sigmoid described by the equation $\frac{dx}{dt} = k \cdot x \cdot (1 - x)$. UNDERWOOD a.o. (1959) used a logarithmic transformation in their work on black rust epidemiology. The writer's preliminary tests indicated that his yellow rust observations might fit better to the logistic curve (logit transformation) than to the integrated normal curve (probit transformation). Consequently the logit transformation has been used in the following.

For the practical application of the logit transformation "logistic paper" was drawn in the same way as the commercial "probability paper" (fig. 42.1). Along the vertical axis at the right hand side the logit $_{PA}$ (from tables in FINNEY, 1952: the

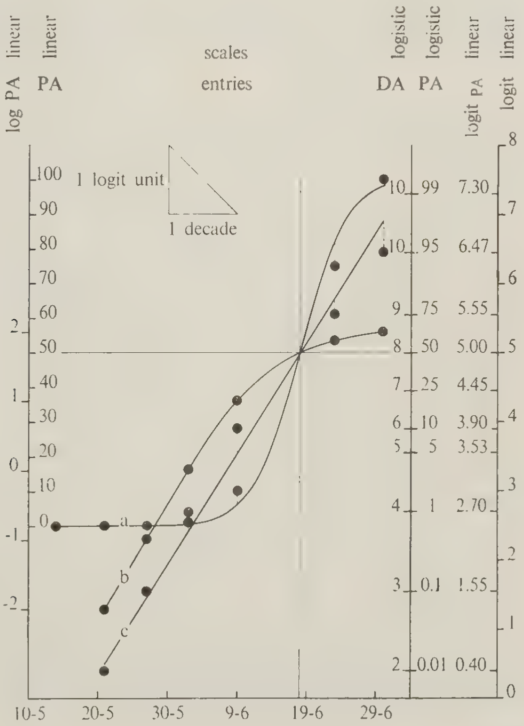


FIG. 42.1
Data from Harvest Queen, 1958, at International Yellow Rust Trial 3460 (Rilland-Bath, Netherlands) plotted as percentage sigmoid (a), logarithmic curve (b) and logit line (c). Several scales have been indicated.

logit Y $= 5 + \frac{1}{2}.\ln \frac{P}{1-P}$, P being a percentage value between 0 and 100%) has been plotted, along the horizontal axis a linear scale is used as a time scale. Scales are adapted so that one logit unit along the vertical axis is equal in length to one decade along the horizontal axis; the procedure facilitates the comparison of slopes of different lines. The observations were plotted on logistic paper and regression lines of logit_{PA} on time were drawn by eye fitting. These regression lines have been called "logit lines". As the DA and PA estimates are rough estimates, there is little need for the exact computation of regression formulas.

TABLE 42.2 Table for the transformation of DA into logit_{PA}. This transformation has been used for the drawing of logit lines.

DA	PA	logit_{PA}
0	0	
+1	0.001	−0.75
2	0.01	+0.40
3	0.1	1.55
4	1	2.70
5	5	3.53
6	10	3.90
7	25	4.45
8	50	5.00
9	75	5.55
first 10	95	6.47
second 10	99	7.30

DA = degree of attack
PA = percentage of attack

Since a logit of PA = 100 does not exist, special values for DA = 10 had to be fixed (table 42.2). In a set of successive observations the first DA = 10 was given the value PA = 95, the second DA = 10 and those following were given the value PA = 99. Though this procedure looks arbitrary, it represents the actual situation better than the formal interpretation of DA = 10 being PA = 100.

A similar difficulty arises in the quantitative evaluation of the DA.s 1 to 3. A DA = 1 at GS = 2.2.3 does not give the same PA as a DA = 1 at GS = 10. As a result of the comparison of several different situations it was concluded that PA = 0.001 is an acceptable average value for DA = 1. This conclusion implies that DA = 2 gives PA = 0.01 and DA = 3 gives PA = 0.1.

The data of the susceptible varieties Michigan Amber, Harvest Queen, Persian and Rubis in the International Yellow Rust Trials were examined after plotting on logistic paper. In many cases there was a remarkable fit between the observed values and the values expected on the assumption of a logistic growth curve of the rust population. Therefore it is thought that the logistic curve is an acceptable approximation of the growth curve of the rust population on the susceptible varieties in the International Yellow Rust Trials.

42.3 The logit line and the logit-linear diagram

The data from the susceptible varieties of the International Yellow Rust Trials, of which four or more observations were available, have been plotted on logistic paper. Logit lines were drawn by eye fitting; a selection of logit lines is presented in fig. 42.3a and 42.3.b.

Logit lines are characterized by their slope and their 50% date; both vary appreciably.

The 50% date, which is the day at which the logit line reaches a value PA = 50 (logit_{PA} = 5), can be regarded as an indication of the severity of infection in the neighbourhood, of the disease pressure in the surrounding of the trial. The earlier the 50% date, the greater the disease pressure (45).

The great variation in the slope of the logit lines was a surprise (in fig. 42.3.a

TABLE 42.3 Differences in slope and 50 % date between the susceptible varieties in the International Yellow Rust Trials (differences between varieties within trials)

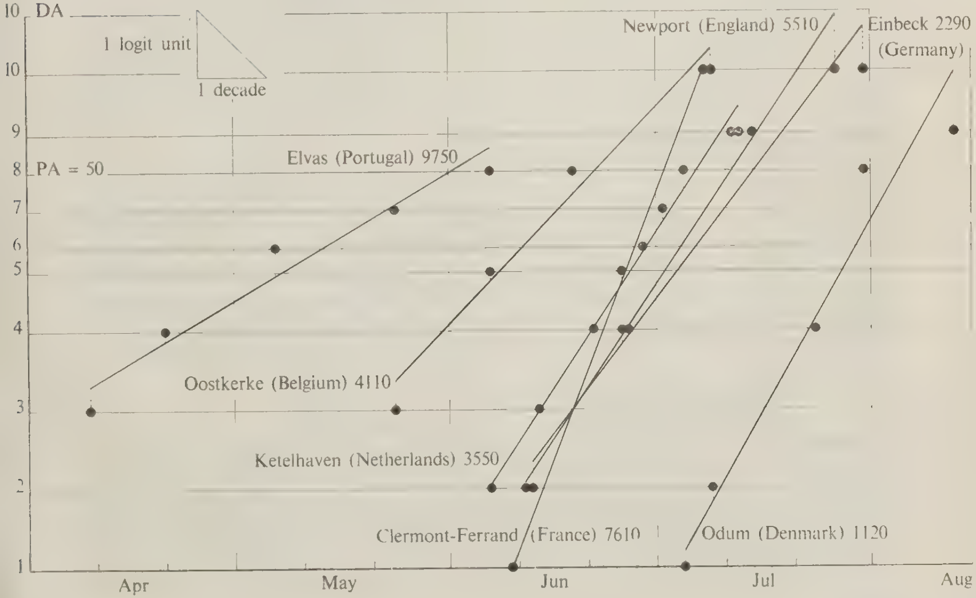
variety	$\bar{d}_s$	$\bar{d}_d$	n
Michigan Amber	— 2.4	— 3.4	11
Persian	+ 1.4	+ 1.5	22
Rubis	+ 1.2	— 0.5	17

$\bar{d}_s$ = average deviation of slope in degrees using Harvest Queen as a standard
$\bar{d}_d$ = average deviation of 50 % date in days using Harvest Queen as a standard
n = number of logit lines over which has been averaged

from 30.5° to 69.0°). Evidently the slope of the logit line has a certain meaning. It suggests that, within limits, the slope is an indication of environmental conditions which can be more or less favourable for the growth of the rust population.

Fig. 42.3.b represents the situation at Elvas, Portugal, in the years 1958 and 1959. When the writer was at Elvas on 9th April, 1958 there was an early focal epidemic of yellow rust which according to information did not develop into a serious attack. SANTIAGO reported that a rather serious epidemic occurred at

FIG. 42.3.a Logit-linear diagram. Logit lines for Harvest Queen, 1958, from different countries. Note that the last observation from each trial is always to the right of the logit line; some lines could have been drawn as steeper lines bending to the right at the top end as in fig. 42.3.b.
DA = degree of attack
PA = percentage of attack



Elvas in 1959. In accordance with these personal communications, the 1959 logit lines show a steep slope and an early 50 % date, whereas the 1958 lines have a gradual slope and a late 50 % date. In each year the logit lines of the three susceptible varieties run more or less parallel. The difference between the years 1958 and 1959 is a doubled slope and a three weeks lag in the 50 % date. Usually exact data on the beginning of the infection are scanty, but in this respect there seems to be little difference between the two years. It is possible, but hardly probable, that the observed differences between years are due to differences between observers.

Comparing the different susceptible varieties Michigan Amber 1959, 1960 (not 1956, 1957), Harvest Queen, Persian and Rubis, there is usually little difference in slope between varieties within trials. The average deviation in slope (within trials) from the standard $\bar{d}_s$ can be computed for the available logit lines, using Harvest Queen as a standard (table 42.3). The resulting differences cannot be regarded as significant.

The average deviation of the 50 % date (within trials) from that of the standard $\bar{d}_d$ is small too, as is shown by the data from table 42.3. Again Harvest Queen has been used as a standard. From the epidemiologic point of view the behaviour of the four susceptible varieties, Harvest Queen, Michigan Amber, Persian and Rubis (when compatible), are approximately identical and differences between these varieties cannot be regarded as significant.

42.4 Deviations from the logit line: susceptible varieties in the International Yellow Rust Trials

Many minor deviations from the logit lines can be found. Some can be attributed to the observer, who lacked training in disease assessment (evaluation of non-pathogenic chlorosis is one of the major disturbants); others can be traced to obviously abnormal conditions of growth, environment or climate. Aberrations are possible as a result of very early or very late infection. The observations of two different observers on the same object seldom fit to the same logit line. For the present, all these errors are accepted as random errors which do not materially influence the result.

A more important deviation is the frequent decrease in the slope of the logit line at the upper end. A decrease of slope to 0° at the level of PA = 99 % is normal, as 99 % is practically the maximum possible infection. A decrease at a lower PA level has, however, a special meaning. It means that the growth of the rust population stops before the substrate is exhausted, either because of a change of weather creating adverse infection conditions or because of a change in host-parasite compatibility. The change in compatibility can be a varietal characteristic and it may, or may not, be induced by a change of weather.

42.5 Deviations from the logit line: Heines VII in the International Yellow Rust Trials

Heines VII was chosen as an example of a commercial variety with intermediate CI (CI = c. 45) on which severe epidemics have occurred. Data of Heines VII and Persian have been plotted in fig. 42.5 from four successive years at one trial, Wieringerwerf 3510. The various Heines VII lines show most of the deviations encountered.

The 1957 growth of the rust population on Heines VII follows the logit line

until early June, when the level DA = 9 is reached. The population growth comes to a stop, though sufficient substrate is available. A hot spell in June probably contributed to this change in the population growth either by changing the infection conditions or by altering the host-parasite compatibility, or possibly by changing both.

In 1958 the rust appears much later and the growth of the rust on Heines VII is so irregular that no logit line has been drawn.

In 1959 the rust on Heines VII appears still later and the population growth is slow. A late 50 % date and a gradual slope are characteristic for the very dry year of 1959.

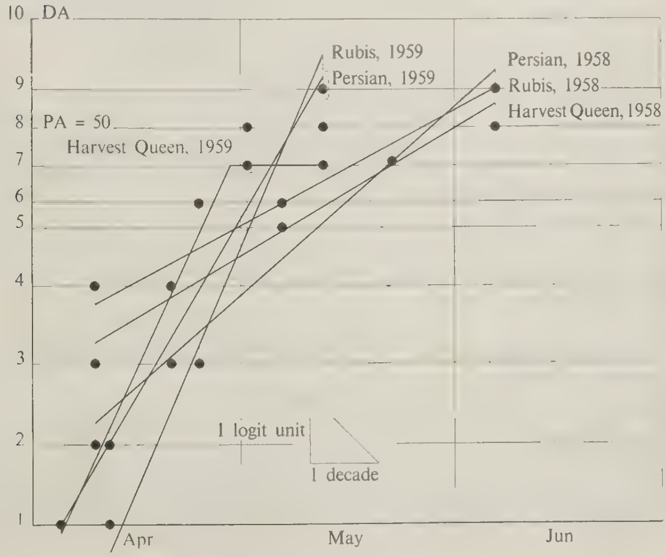
In 1960 the rust was so scarce that no infection on Heines VII was observed.

Usually the rust on Heines VII is later than on the susceptible variety Persian, which has been used as a standard, and more often than not the population growth on Heines VII cannot be adequately depicted by a logit line. When the logit line is applicable to Heines VII it is mostly in the lower half of the growth curve only. On trying other commercial varieties with intermediate CI, similar difficulties were encountered as with Heines VII.

42.6 Deviations from the logit line: Heines VII in farmers' fields

In fig. 42.6 some field data from 1957 have been plotted in the usual way.

FIG. 42.3.b Logit-linear diagram. Logit lines of three susceptible varieties at Elvas (Portugal; International Yellow Rust Trial 9750) in the years 1958 and 1959. The two years differ appreciably in the slopes of the logit lines. Note the typical bend at the top end of the logit line of Harvest Queen, 1959; the other 1959 lines could have been drawn in the same way. The alternative possibilities in drawing logit lines indicate the limitations of this method.
DA = degree of attack
PA = percentage of attack



The data of the fields 7012 to 7018 refer to fields of 30 ha., so that here the term "rust population growth" is more apposite than in the case of the International Yellow Rust Trials, where the plots are no more than 0.5 m^2.

Similar difficulties are encountered as those in the case of the International Yellow Rust Trials. Until April, when a DA = c.7 is reached, the population growth is more or less along straight lines, deviations being probably due to the use of the International Scale for the assessment of DA with its large intervals. In April the lines bend, some going still slightly up, some going down, others remaining level.

It is this bend which is puzzling and which needs further investigation (44.4). It is interesting to note that the data from the 1960 detailed trial, described in 43.2, do not show the characteristic bend when plotted on logistic paper.

42.7 Critical considerations on the logit line

The logistic curve represents the course of the autocatalytical reaction; also it represents fairly accurately the growth curve of bacteria in a limited amount of nutrient broth. The use of the logistic curve and of the logit line is based on several presuppositions among which are the following:

1. at its beginning the growth of the population is limited by the amount of rust only,
2. at its end the growth of the population is limited by the amount of available substrate,
3. the generation time of the rust is constant,
4. the amount of substrate diminishes because of the consumption by the rust and is not replenished,
5. the rust-substrate interaction is constant.

The presuppositions 1 and 2 can be accepted without much difficulty in the case of yellow rust on wheat, except for the restriction that especially at the beginning and at the end of the population growth, in winter and in summer, weather conditions may limit sporulation or infection.

Presupposition 3 is not generally true as the incubation time varies according to the season. The observations from the International Yellow Rust Trials are made usually so late in the season that variations in the incubation time are small and of no importance. In the case of field observations the variations in the incubation time cannot be disregarded.

Presupposition 4 is certainly not true; leaves not only die because of the rust, they may also die a natural death. At the same time there can be a vigorous growth of the substrate, a growth which is variable in time; in other words, there is a shifting host population (43.7).

Presupposition 5 is open to serious criticism; in fact the typical bend in the Heines VII curves suggests that the rust-substrate interaction or compatibility is not a constant factor.

The foregoing remarks are of a general statistical nature; from the agricultural point of view there is also room for criticism especially with regard to the use of data from the International Yellow Rust Trials. Each variety in such a trial covers an area of not more than 0.5 m^2 and it is doubtful whether the population growth in such a small area may be compared to that in large fields. More serious is the consideration that the rust development of a commercial

variety with an intermediate susceptibility may be influenced by the stronger rust development of its highly susceptible companions in the trial.

In view of this criticism, it is surprising to see that the logit line adequately represents the rust population growth on the susceptible varieties in very small plots.

43 A QUANTITATIVE APPROACH

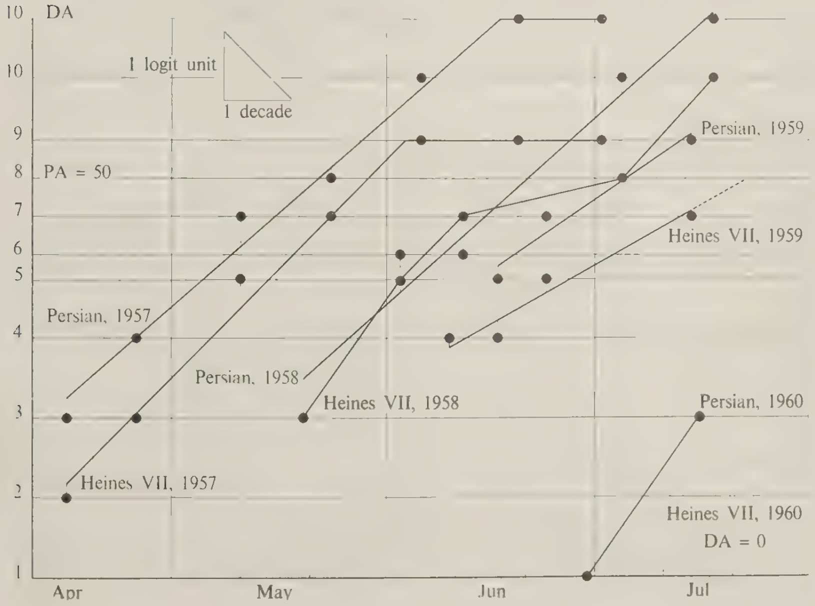
43.1 The wheat in a log-linear diagram

From a small Heines VII plot, grown at the Wageningen trial grounds, two plant samples were taken at regular intervals. Sample A consisted of 4 to 20 plants, sample B consisted of c. 100 plants.

Sample A: Four to twenty plants, thought to be representative of the vegetative development of the wheat, were chosen from the plot. The plants were dissected and the leaves were stuck on to filter paper. The leaves were photocopied, the projected leaf areas in the photocopies were measured with a planimeter. The leaves were numbered in order of plant (I, II, ...), sprout (from main sprout to smallest sprout: a, b, ...) and order of appearance (1, 2, ...).

Sample B: About hundred plants were taken at random from the plot. Plants, sprouts and leaves were numbered in the same way as in sample A.

FIG. 42.5 Logit-linear diagram. A comparison between data of Persian and Heines VII in different years from the International Yellow Rust Trial 3510 at Wieringerwerf (Netherlands).
DA = degree of attack
PA = percentage of attack



For each leaf the percentage of the leaf area covered with sporulating lesions was estimated.

The "leaf position" is determined by sprout letter and leaf number. Thus leaf position a3 indicates the third leaf of the main sprout. Leaves of the same leaf position have approximately the same age and their leaf area data may be averaged. When the leaves along the sprout are numbered from top to bottom, all leaves with the same number belong to the same "leaf layer", independant of their sprout letter (41).

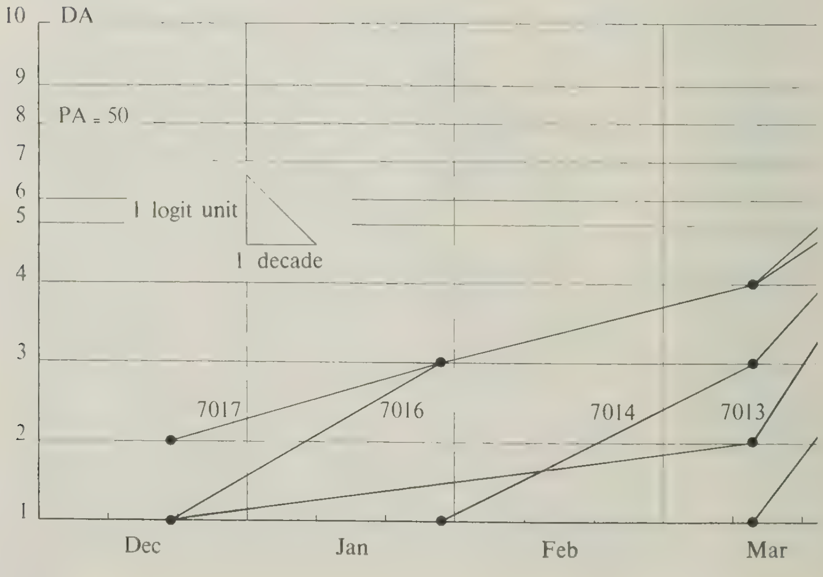
The following data were obtained:

r = sum of rust percentages per leaf position (B)
n = number of living leaves per leaf position (B)
N = number of plants per sample (B)
a = average leaf area (living + dead) per leaf position (A)
l = average living leaf area (green + rusted) per leaf position (A)

To refer these observations to an idealised "standard plant" the following data were computed:

$\frac{nl}{N}$ = average living (green + rusted) leaf area per standard plant

$\frac{ra}{N}$ = average rusted leaf area per standard plant.

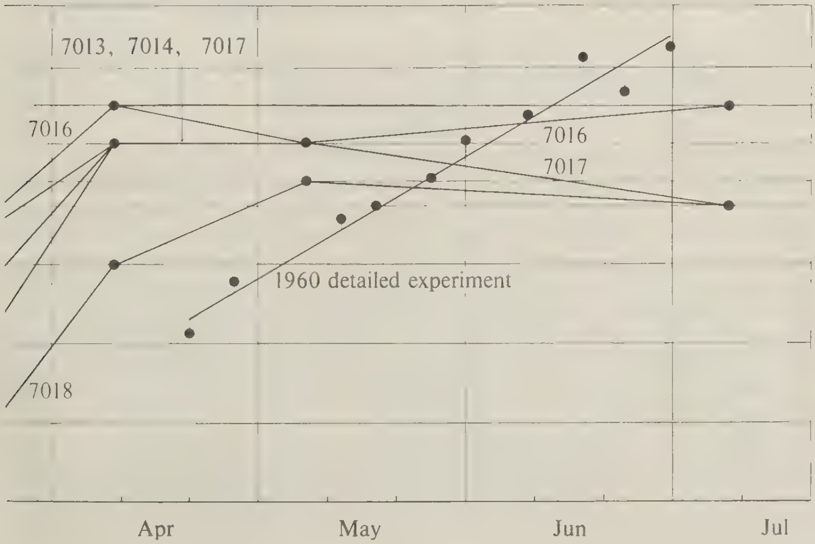


Combining these data of the standard plant with the number of plants per metre drill length and the distance between the drills, LMI and RMI can be easily computed. From the end of May onwards individual plants could no longer be distinguished; the same procedure was applied but "stem" should be read instead of "plant".

For the first growth stages no systematic measurements are available. During germination GS = 0 and LM = 0. The recommended sowing rate for Heines VII on normal clay soils is c. 170 kg. per ha.; the 1,000 kernel weight is c. 45 g.; the germination rate is c. 90 %. These data lead to c. 3,400,000 plants per ha. A few days after emergence each plant has a GS = 1.1.1 and a leaf area = c. 1 cm^2. Consequently at GS = 1.1.1 LMI = $3.4 \cdot 10^6$. In this and in all other growth stages the value of LMI is mainly determined by the number of plants per ha.

The results of the measurements are shown in fig. 43.1, in which the data of 1958 and 1960 have been combined. For comparison the 1934 data of WATSON (1947a) have been plotted on the same scale. There is a fair agreement between the three groups of data. But in early spring the writer's Heines VII showed a richer vegetative development than WATSON's wheat, whereas in 1960 the wheat died nearly three weeks earlier than in 1958. This difference is mainly due to climate and nutritional effects, though in 1960 death may have been hastened by a severe rust infection which has been absent in 1958. The writer's sample for

FIG. 42.6 Logit-linear diagram. Rust population growth on Heines VII/Noordoostpolder/ 7013, 7014, 7016, 7017, 7018 and on Heines VII/1960 detailed experiment. The Noordoostpolder observations refer to 30 ha. fields, the observations were done during the season 1956–57. The 1960 detailed experiment was a small inoculated plot at Wageningen (43.1, 2).
DA = degree of attack
PA = percentage of attack



the determination of the leaf area was small in comparison to that of WATSON and consequently WATSON's data show a more regular course than that of the writer.

The 1958 data have been used to draw a reference curve (fig. 43.1), the autumn section of which is based on the expected growth of 3.4 million plants per ha. The shape of the autumn and winter section of the reference curve is congruent with WATSON's curve. WATSON (1947a, b) demonstrated that LMI is a quantity, variable according to variety, nutritional conditions and year of observation. Great as these variations may be, they are small in comparison to the errors in the rust estimates and therefore these variations are ignored. In some cases the reference curve is slightly changed at the beginning or at the end to fit the curve to particular observations on sowing, emergence or ripening.

43.2 The rust: the 1960 detailed experiment

The 1960 Heines VII plot used for the quantitative description of wheat development was repeatedly inoculated with race W 12 during winter and early spring. Sampling for rust started about 1.5 i after the last inoculation. The sample B was taken at random at regular intervals and the amount of rust was assessed as described in 43.1. In fig. 43.1 the rust curve has been drawn.

The rust curve reveals several interesting points. At the beginning there is an approximately logarithmic increase of the rust population. Later this increase diminishes to 0, but PA is still increasing; at that time the death rate of the substrate is already greater than the growth rate. With an increasing death rate of the substrate the rust population diminishes at first slowly, later rapidly; in this period PA increases to the maximum observed value of PA = 84.5. Then substrate and rust die so rapidly that the process cannot be followed any longer. In the inset of fig. 43.1 the percentage sigmoid is drawn for comparison.

In fig. 42.6 the rust data have been plotted on a logistic scale; they fit reasonably well to a straight line. The typical bend at the top end of the logit line is absent.

This bend is clearly visible in the population growth curves of the 1957 field observations when plotted on a logistic scale, and even more clearly when plotted on the quantitative logarithmic scale (fig. 43.2).

43.3 Oversummering of yellow rust quantitatively expressed

The quantitative expression of yellow rust oversummering is relatively easy, once the basic data are known. It is simple to record the GS.s of the summer carriers of the rust, i.e. the pre- and post-harvest late tillers and the pre- and post-harvest volunteers. It is also relatively easy to estimate the frequency of each category per 10 m. field border length, per m^2 or per 100 m^2. With these data the LMI can be computed. The PA of each carrier category or the frequency of lesions per unit of area can be estimated and the RMI can be computed in the same way. In fig. 43.3.a and b two examples have been given.

In fig. 43.3.a the oversummering of Heines VII/Noordoostpolder/7017 has been depicted. At harvest time rust is present on pre-harvest late tillers; pre-harvest volunteers and post-harvest late tillers are already infected. The RM of the pre-harvest late tillers is destroyed by harvesting. After harvest the pre-harvest volunteers and post-harvest late tillers can be clearly seen; both are rusted. The post-harvest late tillers are completely destroyed by the summer

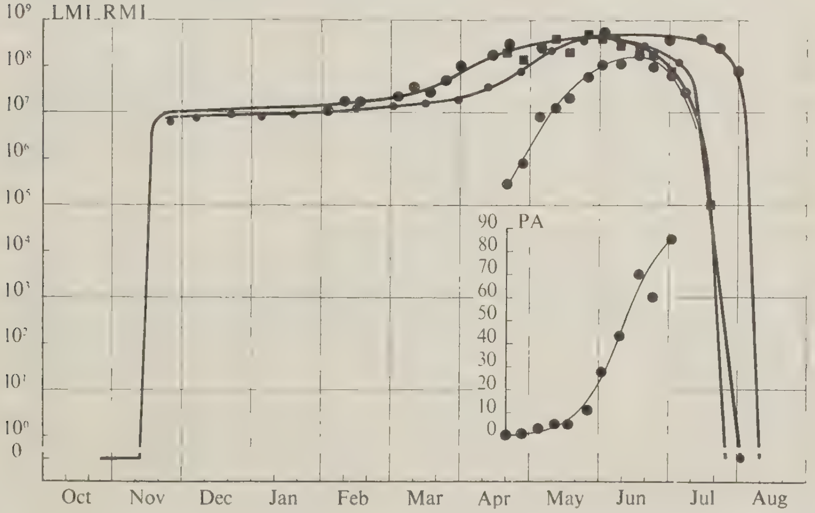
ploughing, the pre-harvest volunteers are reduced to c. 5 %; no rust remained. Post-harvest volunteers appear after the summer ploughing but they do not become infected because inoculum is absent. Autumn ploughing reduces the LMI of the post-harvest volunteers to c. 5 %.

The events of Heines VII/Noordoostpolder/7016 have been given in fig. 43.3.b. Late tillers have not been observed. The summer ploughing reduces LMI of the volunteers to c. 1 % and RMI to c. 5 %; this difference is purely a matter of chance. Whereas in 7016 the difference was 1 % and 5 %, in 7017 this difference was 5 % and 0 %. Autumn ploughing was interrupted by rain fall. Between 30-10-1957 and 20-11-1957 a narrow strip remained unploughed; on this strip one single rust lesion was found, giving a RMI = $10^0 = 1$. The autumn ploughing was of an excellent standard and no volunteer plants could be found. Later some of the buried volunteer plants sprouted again, but the sprouts did not show any rust lesions. As there was some rust left on field 7016 until mid November, early sown Heines VII fields in the surrounding area may have been infected by inoculum from field 7016. When ploughing is only of average standard, LMI and RMI may be increased a hundredfold.

These examples indicate that a quantitative evaluation of yellow rust epide-

FIG. 43.1 Log-linear diagram. The quantitative development of wheat. Reference curves have been drawn for Heines VII/1958 detailed experiment and Heines VII/1960 detailed experiment. The rust curve of the 1960 detailed experiment has been drawn in two ways: as a log curve on a logarithmic scale and as a percentage curve on a linear scale (inset).

—● = LMI, 1958 detailed experiment
—■ = LMI, 1960 detailed experiment
—• = LMI, WATSON's data, 1934 (WATSON, 1947a)
—● = rust observations, 1960 detailed experiment
LMI = leaf mass index
RMI = rust mass index
PA = percentage of attack



miology is well possible. They show the great annual fluctuation of the rust population, which is in the range of 10^8.

The summer of 1957 was a relatively wet summer but it was not especially favourable to the oversummering of yellow rust. A RMI of 10^0 to 10^2 must be regarded as sufficient for the oversummering of the rust population, but it is doubtful whether it is sufficient to cause a severe epidemic. In the summer of 1956 RMI.s must have been much higher; adequate summer observations are, however, not available. On 12-11-1956 a volunteer crop of Heines VII with a LMI = 6×10^6 and a RMI = $4{,}5 \times 10^6$ was found in the Noordoostpolder. High RMI values have also been observed in 1960. The field Triumph/Oostelijk Flevoland/0090 gave the following results on 12-9-1960: LMI (mainly volunteers) = 3.1×10^6, RMI (on late tillers only) = 1×10^2.

43.4 The quantitative effect of mature plant resistance

The effect of mature plant resistance has already been demonstrated in fig. 24.24, where observations have been plotted on a linear PA scale. Whereas the PA of Heines VII increases, the PA of Leda decreases, both varieties growing under the same infection conditions.

An illustrative example is represented in fig. 43.4.a. In the autumn of 1956 a field of Carstens VI/Noordoostpolder/7011 was heavily infected by an adjacent Heines VII volunteer crop. The RMI of Carstens VI rose rapidly, then stopped at a relatively low level and began to decrease in April, when the mature plant resistance came into being. In July no yellow rust has been observed. The oversummering is visualized in fig. 43.4.b. Because of the mature plant resistance there was no inoculum to infect the post-harvest late tillers and volunteers.

In fig. 43.4.a the rust curve for Heines VII/Noordoostpolder/7016 has been given for comparison; the first infection was less intense than that of Carstens VI, but the rate of increase was greater. It is hardly necessary to point out that this apparent difference in susceptibility cannot be reproduced in the greenhouse where seedlings of Carstens VI and Heines VII were equally susceptible to the isolate tested. Examples, similar to that of Carstens VI, could be given for Flamingo infected with the Peko race. In the case of Flamingo the RMI never reaches 0 level because of the presence of a small percentage of very susceptible plants in this variety, but oversummering of the Peko race on Flamingo has never been observed, the RMI at ripening time being probably too low to cause a frequent infection of the volunteer crop.

43.5 Examples of special quantitative effects

Any given rust situation can be expressed quantitatively in LM and RM (NB: for the difference between LM and LMI or RM and RMI see paragraph 41). Field Heines VII/Noordoostpolder/7012 measuring 30 ha. was undersown with Yellow Trefoil. Therefore the field was not summer ploughed. Estimates were as follows:

date	LM	RM
13- 8-1957	1.2×10^5 cm²	3×10^3 cm²
2-10	4.5×10^6	3×10^3
14-11	7.2×10^6	7.2×10^5

Autumn ploughing was done on 30-11-1957. The work was well done, but

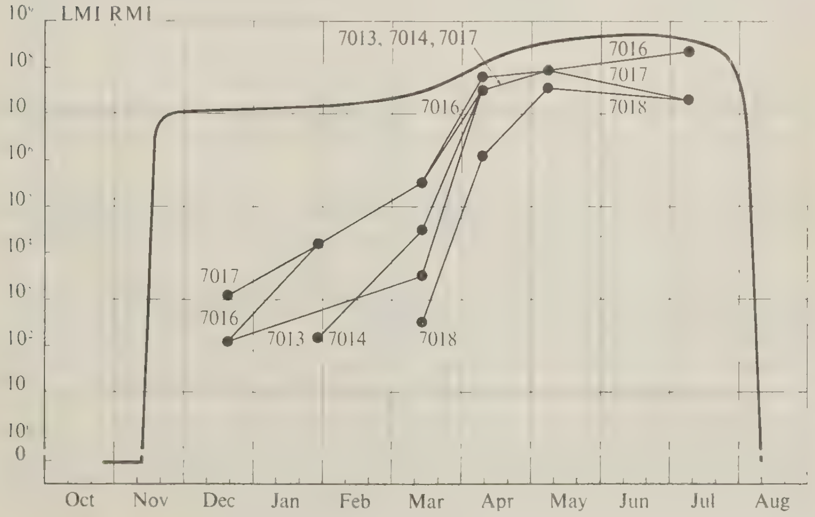
owing to the thick growth of Yellow Trefoil the soil was not always completely turned over. In January the situation was a follows:

date: 21- 1-1956 LM = 3 $\times 10^4$ cm² RM = 7.5 $\times 10^2$ cm²

In some fields of the reclamation area wheat was cut in July to make place for farm yards of c. 1 ha.; the cut wheat sprouted again and ripened one month later than the normal crop (35.2). Because this land had not been ploughed, many self sown plants infected with rust oversummered and overwintered. The farm yard of field Heines VII/Noordoostpolder/7017 was visited on 21-1-1958: LM = 6 $\times 10^5$ cm², RM = 1 $\times 10^4$ cm². For the rest of the well-ploughed field the data were: LM = 2 $\times 10^3$ cm², RM = 0 cm². For another field the data were: farm yard, LM = 9 $\times 10^5$ cm², RM = 1 $\times 10^3$ cm²; for the rest of the well-tilled field the observations amounted to: LM = 6 $\times 10^3$ cm², RM = 2.4 $\times 10^1$ cm². The fields measured 30 ha. The newly sown Carstens VI crops in the neighbourhood were all moderately infected. It is beyond doubt that the inoculum came from the adventive wheat of the farm yards, since these produced at least a thousand times more rust than the rest of the fields.

It is of practical interest to estimate the relative danger of race nurseries which, in the writer's experiments, measured c. 30 m². Race nurseries are inoculated in March. The first sporulation is in April. At that time in each race nursery 5 hassocks of c. 20 plants with a GS = 3 show a PA = c. 5: LM = 3 $\times 10^5$ cm² and RM = 5 $\times 10^2$ cm². In a year with a severe epidemic a RM of 5 $\times 10^2$ cm²/ha. is already attained in December (fig. 43.2). At the end of May

FIG. 43.2 Log-linear diagram. The development of the rust population in the field, Heines VII/Noordoostpolder/7013, 7014, 7016, 7017 and 7018; data refer to 30 ha. fields during the season 1956–57. The RMI curves show the typical bend in April.
—— = LMI, leaf mass index
—— = RMI, rust mass index



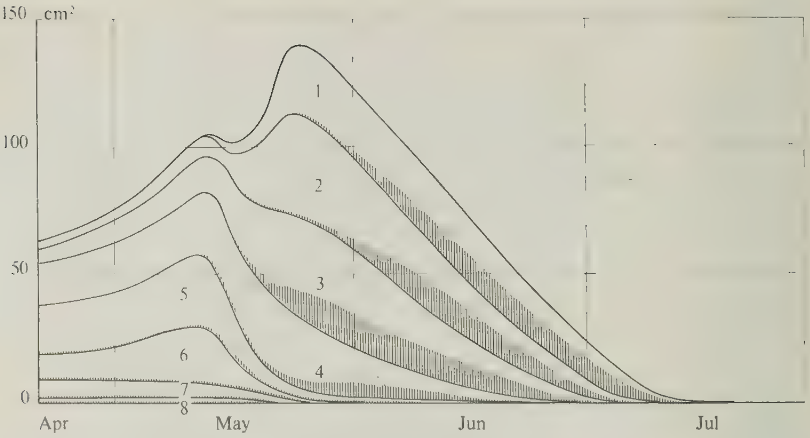


FIG. 43.7 Sketch of the development of the leaf mass LM of a "standard plant" in cm^2 (for details see 43.1). The LM of the different "leaf layers", numbered from top (flag leaf) to bottom, is indicated. The rust mass RM, separated into the RM.s of the different leaf layers, is indicated by shadowing.
This sketch is based on data from the 1960 detailed experiment.

a race nursery normally reaches its maximum level of infection. Half of the hassocks have a PA = 100: LM = 1.3×10^6 cm^2 and RM = 6.5×10^5. In an epidemic year a RM = 6.5×10^5 cm^2/ha. is already present at the beginning of April (fig. 43.2) and hundreds of hectares of rusted wheat area are a more potent source of infection than a few isolated race nurseries. It is concluded that race nurseries cannot be the source of epidemics; when well isolated, they do not endanger the neighbouring wheat fields. This conclusion on the quantitative effects of race nurseries does not exclude the possibility that they are instrumental in the establishment of new races.

43.6 The Heines VII epidemics in a log-linear diagram

All relevant material on the Heines VII epidemics in the past ten years has been combined into one graph, visualizing the quantitative development of Heines VII and its rust in the Netherlands.

To determine the quantitative development of the host, use has been made of the reference curve and of the Heines VII acreages. The amount of oversummering LM has been estimated, taking into account the available observations on oversummering and the general weather conditions.

To estimate RM (irrespective of races) all available information has been combined. This information consists of the International Yellow Rust Trials, the data of the Rust Survey of the Plant Protection Service (VEENENBOS, 1955, 1956; HULSHOFF, 1958; HULSHOFF & DIJKSTRA, 1959, 1960), the writer's field observations and other relevant information.

For each month LM and RM of the Netherlands were computed. To adjust the weight of the respective observations all data were computed per province and then summarized over provinces. The result is presented in fig. 43.6, which gives a picture of the rise and decline of the Heines VII epidemics.

43.7 The shifting host population

Old leaves die and new leaves appear. The substrate changes continuously and the rust has to follow the shifting host population. The rust population has to restore itself all the time.

In fig. 43.7 the LM of the standard plant (43.1) has been sketched, separated into the LM.s of the individual leaf layers. Towards the end of shooting new leaf layers appear in rapid succession, whereas the lower leaf layers die. Within two weeks, the composition of the LM changes completely.

The position of the rust in the 1960 detailed experiment is indicated in the sketch. In this example the change of the position of the rust is not impressive. When a severe attack is present in early May, the rust population has to renew itself entirely within a short time.

44 THE USE OF THE i-TIME SCALE

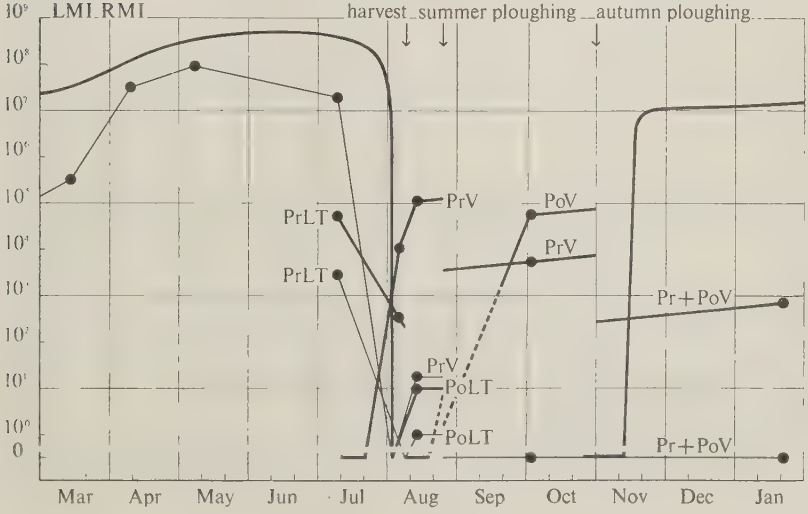
44.1 The i-time scale

The logit line and the quantitative approach are suggestive illustrations of the development of epidemics, but a biologically more correct approach will be made when the linear time scale is transformed into an i-time scale.

FIG. 43.3.a Log-linear diagram. Oversummering of yellow rust on Heines VII/Noordoostpolder/7017 during the summer of 1957. Pre- and post-harvest late tillers and volunteers are infected. Summer ploughing reduces the amount of rust to 0.

—— = LMI, leaf mass index
—— = RMI, rust mass index
PrLT = pre-harvest late tillers
PoLT = post-harvest late tillers
PrV = pre-harvest volunteers
PoV = post-harvest volunteers

The development of the LMI of a neighbouring field during the season 1957–58 has been indicated.



In the i-time scale the incubation time i is the unit of time irrespective of its length in days. The i-time scale has already been illustrated by the lower part of the slide rule for the estimation of the potential number of generations per season (fig. 32.3.d).

The wheat reference curve of fig. 43.1 can be adapted to the i-time scale. It must be remembered that the i-time scale has been drawn on the basis of temperature normals, so that in individual years considerable deviations are possible. For the present discussion these deviations have been ignored.

44.2 Field observations in the log-i diagram

Field and trial observations are plotted on the i-time scale in fig. 44.2.a, b and c. Data of Heines VII/Noordoostpolder/1957 have been plotted in fig. 44.2.a. The characteristic bend at the upper end of the curves is accentuated by the i-time scale. The abruptness of the bend is partly due to the lack of observations (see also 46). A later onset and more gradual slopes characterize the data from Heines VII in 1958 and Flamingo in 1959.

The data of fig. 42.5 are shown again in fig. 44.2.c. The form of the curves of the susceptible variety Persian and the commercial variety Heines VII in the International Yellow Rust Trials is not essentially different from that of the Heines VII field observations.

44.3 The logit-i diagram

The curves of a few fields, of which an adequate number of observations per field was available, are shown in fig. 44.3.a and b.

The fields Heines VII/Noordoostpolder/7016 and 7017 show approximately straight lines with a steep slope, which bend abruptly. The fields Heines VII/Haarlemmermeerpolder/8070 and 8171 and the field Flamingo/Noordoostpolder/9186 show approximately straight lines with a more gradual slope than the fields 7016 and 7017. The data of the 1960 detailed experiment also fit fairly well to a straight line.

The amount of data is too small to come to any definite conclusion; the results suggest that the logit-i diagram may be useful in obtaining straight lines in those instances where the rust population starts to build up late in the season, or where an early infection is followed by a relatively slow growth of the rust population.

The sharp bend in the curves of the fields 7016 and 7017 still requires an explanation. The most plausible explanation is that in the months April and May the production of fresh leaf is at its maximum. Quantitatively the newly produced leaf area is about half of the total leaf area. This newly produced leaf area is younger than one i and therefore cannot yet show any sign of infection. Therefore in late April and in May the maximum possible PA = c. 50 %. When all leaves have appeared the rust population can overcome the temporary limit of 50 %, as is clearly demonstrated in the 1960 detailed experiment. That fields 7016 and 7017 do not show values higher than 50 % is probably due to the lack of observations between early May and early July.

In this context it is interesting to observe that during a severe epidemic, as in 1957, the upper leaf layers start to sporulate at the tops of the leaves, the sporulating area increasing towards the base at about the same speed as the leaves

appear. Apparently fresh leaves are infected as soon as they appear under conditions of a surplus of inoculum. The downward extension of the sporulating area was not due to a growth of the lesions but to new infections: this could be read from the typical lesion pattern.

45 THE RUST PRESSURE

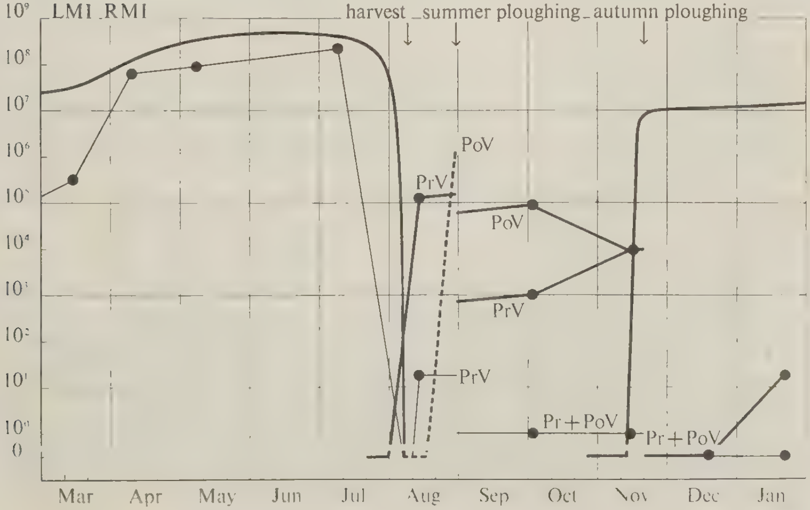
"Disease pressure" is a much used but ill-defined term. The disease pressure in a breeder's nursery with many susceptible varieties is greater than that in a farmer's field. When the nursery is artificially infected, the disease pressure is increased. During a severe epidemic the disease pressure is at its maximum.

A useful way to measure the disease pressure, in this case the yellow rust pressure, at different localities may be found in the foregoing pages. The International Yellow Rust Nurseries are grown in many places in Europe; they contain two or more highly and universally susceptible varieties. The rust development can be adequately described by the logit line. One of the character-

FIG. 43.3.b Log-linear diagram. Oversummering of yellow rust on Heines VII/Noordoostpolder/7016 during the summer of 1957. Pre- and post-harvest volunteers are infected. Late tillers have not been observed. Summerploughing reduces LMI and RMI considerably. Autumn ploughing was interrupted by bad weather; on the unploughed part of the field (ca. 1 ha) several plants remained but only one single yellow rust lesion could be found (RM = 1; RMI = 1 = 10^0). When the whole field was ploughed, no rust remained and even the volunteer plants temporarily disappeared.

—— = LMI, leaf mass index
—— = RMI, rust mass index
PrV = pre-harvest volunteers
PoV = post-harvest volunteers

The development of the LMI of a neighbouring field during the season 1957–58 has been indicated.



istics of the logit line is the 50 % date, which can be determined more or less exactly. Sometimes it has to be found by extrapolation. For the extrapolation on the basis of one or two observations the slope of the logit line is necessary. To stay on the safe side, the average slope of the available logit lines has been used (50° for Persian in 1957); since the available logit lines necessarily come from trials with a relatively high disease pressure, the extrapolated 50 % date will usually be on the early side, which implies that the disease pressure will be rarely underestimated.

The 50 % date itself is not an appropriate measure for the rust pressure. It is preferable to determine the time lapse between the 50 % date and the harvest date. Average harvest dates from many localities are known from an unpublished enquiry by the Netherlands Grain-Centre. Since there are great fluctuations in harvest time and since the 50 % dates usually cannot be determined exactly, the time between 50 % date and harvest date is expressed in decades.

The measure for rust pressure as developed here, the "rust pressure value", is the time in decades between the 50 % date of a highly and universally susceptible variety (usually Harvest Queen) and the harvest date. The greater this rust pressure value, the higher the rust pressure; negative values indicate that the extrapolated 50 % date is later than harvest. Map 45 is an example of a rust pressure map.

46 DISCUSSION

The log-linear diagram is the type of diagram which is easiest to read; it can be used to indicate definite quantities of host and parasite. The log-i diagram has the advantage of the i-time scale but is more difficult to read than the log-linear diagram.

The logit-linear diagram is especially useful for very susceptible varieties which have been infected so late in the season that i is practically constant. This type of diagram does not deal with quantities but with proportions. The logit-i diagram is useful for field observations over a long period during which i is not constant.

In the logit-i diagram some of the field observations fit reasonably well to the expected straight line; curves of other fields show a characteristic sharp bend at the upper end, which can at least partly be explained by the curious growth rhythm of wheat giving a temporary upper limit of c. 50 % to the PA.

The logit line is described by the equation $Y = 5 + \frac{1}{2} \cdot \ln \frac{P}{1-P}$ in which $O < P < 1$. This equation is derived from the logistic or autocatalytic function.

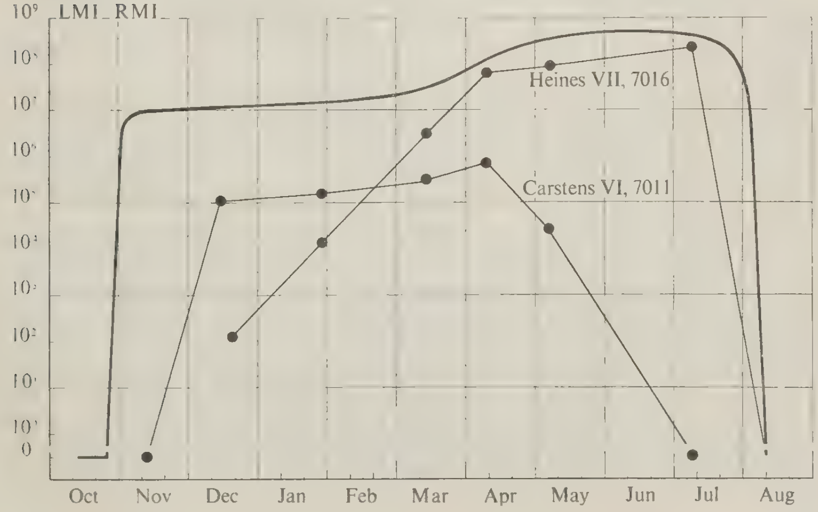
In the curve described by the autocatalytic function (fig. 42.1) five phases may be discerned. In the lower linear part below P = 0.01, the value 1–P can be ignored, being practically equal to 1; in this phase the logit Y is a logarithmic function of P. The other phases are the lower upward bend, the steep nearly linear increase, the upper downward bend and the upper horizontal phase when $P > 0.99$; this last phase is of no interest here. The interesting point is that the observations from all four phases ($0.000{,}01 < P < 0.99$) fit more or less to the logit line. In other words, the logistic function is an adequate mathematical description of the population growth of the rust.

The writer's graphical approach is not essentially different from VAN DER PLANK's (1960) algebraical approch. VAN DER PLANK's discussion starts with the equation $\frac{dx}{dt} = k.x.(l\text{–}x)$, which is a simplified form of the logistic function differentiated to t. To include the effects of temperature (T), humidity (H), susceptibility (S) etc. VAN DER PLANK rewrites his equation in the form $\frac{dx}{dt} = k.x.(l\text{–}x).f(T, H, S \ldots)$, a form which suggests much but helps little. In the writer's logit-i diagrams fT is at least partially replaced by the i-time scale, fH is probably depicted by differences in slope (fig. 42.3.b), whereas fS is visualized by changes in slope.

The relation between the growth curve of yellow rust and the logistic curve is an empirical relation; no explanation can be given. Other functions may be found which describe the growth of the yellow rust population better than the logistic function.

It will be necessary to construct a mathematical model of the rust population growth which can be tested experimentally. In the meantime it will be interesting to reverse the argument and to start with the postulate that the growth of the yellow rust population is adequately represented by the logistic function. It will then be the task of the epidemiologist to explain differences in slope and 50 % date and sudden changes in the slope of logit lines.

FIG. 43.4.a Log-linear diagram. The quantitative effect of mature plant resistance; season 1956–57. In the autumn of 1956 a field of Carstens VI/Noordoostpolder/7011 was severely infected by rust from an adjacent field with a heavily rusted volunteer crop. After a rapid increase, the rust population remained at a relatively low level and started to decrease early in the season. For comparison a growth curve of a rust population on Heines VII/Noordoostpolder/7016 has been given.
—— = LMI, leaf mass index
—— = RMI, rust mass index



The writer expresses the hope that the foregoing suggestions will help to develop quantitative epidemiology into a well-documented and theoretically sound branch of phytopathology.

5 SUMMARY

1 Introduction

In an introductory chapter, data have been assembled on the North-west European wheat area (11), on the wheat plant and wheat culture, and on "residual wheat" in the so-called "wheat-free period" (12). In the Netherlands and in the surrounding area, the fields are at no time completely without fresh green wheat plants. The symptoms of yellow rust were described summarily (13), the methods of rust assessment were described in detail (13). Data on techniques (14), on the International Yellow Rust Trials Project (15) and on the field observations (16) were provided.

2 Physiologic specialization and epidemiology

The physiologic specialization on the generic level, studied in the mature plant stage, leads to the acceptance of the taxonomic unit *forma specialis* (22, 25.4, 26). This does not mean that no foci of wheat rust races can be found on *Agropyrum*, but these are rare and small and of negligible importance to the epidemiology of yellow rust on wheat (22).

Race identification on seedlings in the greenhouse was discussed at some length (23). The importance of a good regulation of irradiation, during the identification as well as during the multiplication of inoculum and the growth of the test plants, was stressed (23.3). Under Wageningen conditions only four differentials were reliable: Vilmorin 23-W, Heines Kolben-W, Carstens V-W and Chinese 166-W (23.4). With these four differentials a temporary race identification key has been made (23). These results are in partial contrast to those of Fuchs (1960).

A detailed study of the physiologic specialization on mature plants in the field has been made (24). A technique was developed in order to demonstrate this form of physiologic specialization (14.6, 24.2). Several "field races" have been described (24.4). Recent epidemics have been analysed with reference to these field races (24.5).

The genetic aspects of race-variety compatibility have been analysed (25). In a speculative approach an attempt has been made to identify genes, using a modification of a technique introduced by Person (1959; 25.2). At least two types of resistance genes are present, one type conditioning resistance in all growth stages of the wheat ("overall resistance"), the other conditioning resistance in the mature plant only ("mature plant resistance"). Both types of resistance occur in commercial varieties, with some prevalence of the mature plant type of resistance. Genes for virulence of the rust can be compatible with either type of resistance of the wheat. A race non-specific "rest resistance" has been tentatively described and a method for assessment has been indicated (25.3).

The incubation time i shows marked fluctations depending on temperature; extreme values being 11 and 180 days (32.2). The "potential number of rust generations" per year N_g c. 17, the potential number of rust generations during the vegetation period is c. 9. A slide rule was designed for the estimation of the number of generations for any chosen period (32.2). Random variations in i between leaves inoculated on the same day also occur (32.3).

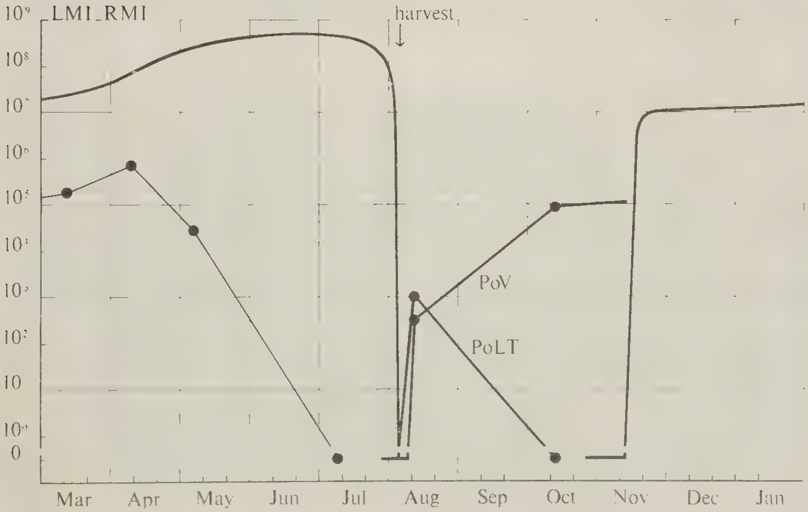
Yellow rust overwinters in the leaves of the new sown winter wheat crop and of self sown plants; it rarely sporulates during winter (33).

Focus formation was studied in detail (34). Successive sporulation waves in a focus starting with one sporulating leaf, could be demonstrated up to the fourth generation (34.2); then the increase in the amount of rust became continuous due to the overlapping of generations. Wider implications of focal infection are discussed (34.3,4). The intensity of endemics is variable according to climate and cultural practices (34.6).

Yellow rust oversummers on pre- and post-harvest late tillers and volunteer plants (35.2), and possibly also on late crops in the Alps at c. 1,000 m. altitude

FIG. 43.4.b Log-linear diagram. Mature plant resistance and the oversummering of yellow rust; summer 1957. Carstens VI/Noordoostpolder/7011 was heavily infected in the winter. The rust disappeared completely when the mature plant resistance came into being. Though post-harvest late tillers and volunteers were abundant, no yellow rust oversummered in the field because of the absence of inoculum; brown rust, however, oversummered in great quantities.

——— = LMI, leaf mass index
——— = RMI, rust mass index
PoLT = post-harvest late tillers
PoV = post-harvest volunteers
The development of the LMI of a neighbouring field during the season 1957–58 has been indicated.



(35.3). Grasses rarely act as summer hosts and the amount of inoculum on grasses is negligible (35.4).

Spore dispersal over short and medium distances occurs frequently (36.1, 2). Spore dispersal over long distances occurs regularly. In Europe it could not be established whether the long distance spore dispersal was a one step or a multi-step dispersal. Outside Europe both types of dispersal occur up to distances of 1,000 to 2,400 km. (36.3). The influence of weather types (37.2) and of acreage of the host variety (39) are briefly discussed.

4 Quantitative epidemiology

An attempt is made to describe yellow rust epidemiology in quantitative terms and to give an adequate graphical representation of the development of the rust population. Four types of diagrams have been tried: the logit-linear diagram (42.3), the log-linear diagram (43.1), the log-i diagram (44.2) and the logit-i diagram (44.4). It is possible to express any given amount of wheat or rust quantitatively, using the terms "leaf mass" LM and "rust mass" RM or "leaf mass index" LMI and "rust mass index" RMI (41).

Successive observations from one object, plotted on logistic paper (42), fit reasonably well to a straight line, especially when the i-time scale is used (44).

The disease pressure of yellow rust is evaluated using a "rust pressure value" (45); rust pressure values for 1957 have been mapped in map 45.

6 SAMENVATTING

0 Voorwoord

De aanleiding tot het onderzoek, waarover deze publicatie handelt, is een ernstige gele-roestepidemie op Heines VII, die een schade van ongeveer *f* 5.000.000 veroorzaakte. Organisatie en financiering van het onderzoek worden besproken.

1 Inleiding

11, 12 Na een kort overzicht van de plaats van Nederland in het Noordwest Europese tarwe-gebied (11) worden de tarweplant en enkele aspecten van de tarweteelt behandeld (12). Naast de normale tarweplant worden onderscheiden de "knipaartjes" (pre-harvest late tillers), „doorwas" (post-harvest late tillers) en opslag (self-sown plants, volunteers). De „opslag van voor het maaien" groeit meestal in „aarkoppen", dit zijn plantenkluwens ontsproten aan tegen de grond geslagen aren; zij kunnen voor de oogst reeds geïnfecteerd zijn. Korrels, uitgevallen tijdens de oogstwerkzaamheden, geven de „opslag van na het maaien". „Adventief-tarwe" groeit bij mestvaalten, op bouwplaatsen, langs wegen e.d. Bijzondere aandacht verdient de „tarwe-vrije" periode in de zomer (12.22). De lengte van deze periode in verschillende delen van Europa is verschillend (kaart 12.22). In een aantal gebieden is deze periode niet geheel tarwevrij, aangezien knipaartjes, doorwas en opslag voorkomen en een residu van groene planten geven, een verschijnsel dat vooral optreedt in gebieden met veel zomerregen. De wijze van ploegen, het gebruik van hopperupsklaver of rode

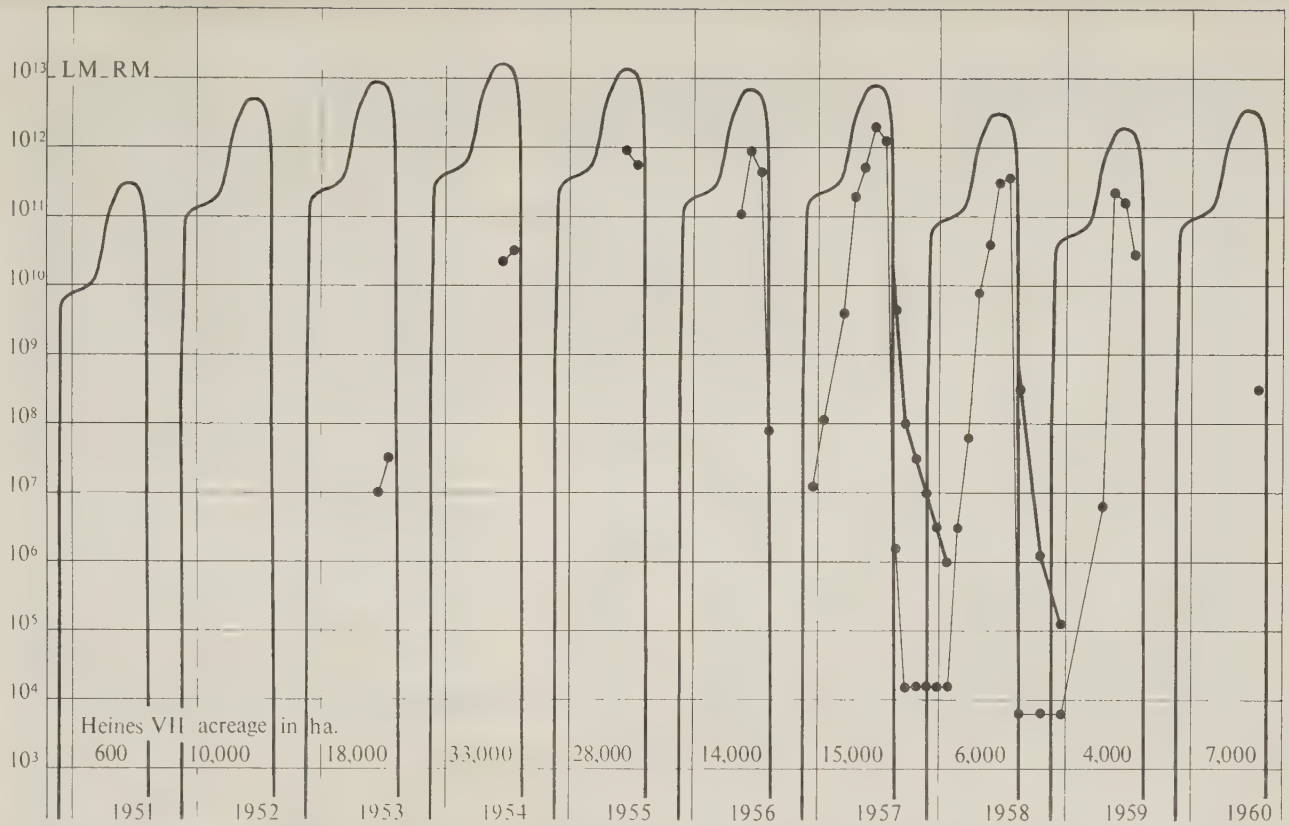


FIG. 43.6 Log-linear diagram. Heines VII and the Heines VII epidemics in the Netherlands. The LM curve covers all Heines VII grown in the Netherlands during the years 1951–1960; the country's RM data have been computed for each month on the basis of all relevant information. Detailed summer observations were available only for 1958 and 1959. LM = leaf mass RM = rust mass

klaver voor groenbemesting of hooiwinning en andere meer regionale praktijken beïnvloeden de hoeveelheid residu-tarwe gedurende de „tarwe-vrije" periode. De FEEKES-schaal wordt gebruikt voor de bepaling van het ontwikkelingsstadium GS van de tarwe (tabel 12.11).

13–16 Een beschrijving van de belangrijkste symptomen van de gele roest in kas en veld is gegeven, de internationale schalen voor de bepaling van het aantastingstype IT in de kas en te velde en van de aantastingsgraad DA te velde zijn besproken (13). Een exposé wordt gegeven van de gebruikelijke technieken, waaronder de isolatie, de instandhouding en de vermeerdering van roestherkomsten in de kas, het maken van één-sorusculturen, de plantebestraling in de kas en het bewaren van herkomsten in vacuo. De techniek van de roesttuinen (rust nurseries; 14.5) en van de fysio-velden (race nurseries; 14.6) is behandeld. Tenslotte worden het Internationale Gele Roest Vangsortimenten Project (15, kaart 11.3.a, b, c) en de veldwaarnemingen (16) besproken.

2 Fysiologische specialisatie en epidemiologie

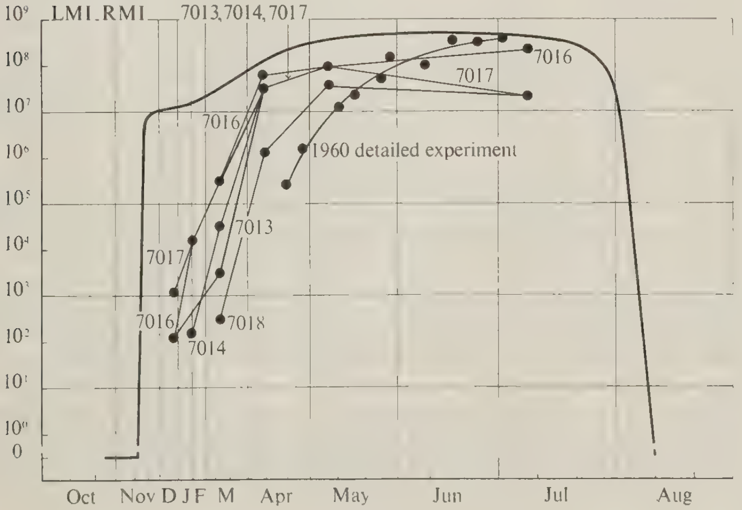
21,22 Een aantal technische termen wordt gedefinieerd (21). Het bestaan van een fysiologische specialisatie op gastheergeslachten wordt bevestigd. Eigen proeven, veldwaarnemingen en literatuurgegevens geven aanleiding tot het onderscheiden van ten minste vier *formae speciales*, de *f.sp. agropyri*, *dactylidis*, *hordei* en *tritici*. De mate van specialisatie is verschillend, de *f.sp. dactylidis* of kropaar-roest is sterk gespecialiseerd en wordt niet op andere geslachten gevonden, de *f.sp. tritici* of tarwe-roest wordt bij gelegenheid ook gevonden op gerst en kweek. Het gevaar van gele roest op grassen voor de tarweteelt wordt afwezig of uiterst gering geacht, hoewel bij uitzondering wel eens haardjes van tarweroest op kweek gevonden zijn.

23 De resultaten van de fysio-determinatie in de kas te Wageningen en die te Braunschweig worden vergeleken (23.1, 2). Milieu-invloeden zijn zeer belangrijk bij het tot stand komen van de reactietypen; de invloed van temperatuur, luchtvochtigheid, bestraling en inoculum worden nagegaan aan de hand van eigen waarnemingen en literatuurgegevens (23.3). Onder de heersende Wageningse omstandigheden zijn Vilmorin 23, Heines Kolben, Carstens V en Chinese 166 goede toetsrassen. In Wageningen differentieert Carstens V goed en Webster slecht, maar in Braunschweig is het omgekeerde waar, zodat het mede hierdoor helaas niet mogelijk is gebleken de Braunschweigse toetsingsresultaten in Wageningen nauwkeurig te reproduceren. Besloten werd tot het opstellen van een Wageningse determineertabel met een tijdelijk karakter, gebaseerd op de vier betrouwbare toetsrassen (tabel 23.6.a); het verband tussen de Braunschweigse en de Wageningse fysios is gegeven in tabel 23.6.b. Om de plaats van determinatie aan te duiden zullen de rasnummers voorafgegaan worden van de letters B voor Braunschweig, C voor Cambridge en W voor Wageningen. Behalve de rassen van het toetssortiment zijn een veertigtal andere rassen in de kas getoetst tegen een twintigtal herkomsten (tabel A.23.5, A.23.6.b). De resultaten van de fysio-determinaties in de kas zijn van geringe waarde voor het verkrijgen van een beter inzicht in de epidemiologie van de gele roest te velde (23.7).

24 De fysiologische specialisatie van de gele roest te velde is in detail bestudeerd met een speciaal daartoe ontworpen techniek (24.1, 2, 3). De gegevens worden ontleend aan de fysio-velden en vangsortimenten; zij zijn omgerekend en gemiddeld met als eindresultaat voor iedere fysio-ras (race-variety) combinatie een eindcijfer, de compatibiliteitsindex CI. Deze index is een getal tussen 0 en 100, dat de compatibiliteit van de fysio-ras combinatie aangeeft. 0 betekent incompatibiliteit van de combinatie, dit is resistentie van de gastheer of avirulentie van het fysio; 100 betekent maximale compatibiliteit van de combinatie, dat wil zeggen volledige vatbaarheid van het ras of grote virulentie van het fysio. CI is een verhoudingsgetal, dat de compatibiliteit van een bepaalde fysio-ras combinatie vergelijkt met de combinatie fysio-Michigan Amber, waarbij de laatste combinatie steeds op 100 gesteld is. CI heeft uitsluitend betrekking op de reactie van de volwassen planten, dit zijn planten met een ontwikkelingsstadium 9 of meer. Een aantal veld-fysios en -populaties worden beschreven en vergeleken met kas-fysios (24.4, tabel 24.42 en A.24.42). De geschiedenis van een aantal recente epidemieën wordt nagegaan in verband met de nieuwe gegevens over de fysiologische specialisatie te velde (24.5). Het blijkt, dat de fysiologische specialisatie op de volwassen plant een goede basis is voor de verklaring van aantastingsbeelden uit de praktijk, waargenomen tijdens epidemieën.

25 De genetische aspecten van de compatibiliteit worden nader onderzocht. Het eerste blad, de halmbladeren, de stengel en de aar kunnen sterk verschillen in resistentie; de verschillen zijn fysio-specifiek (25.1). Er zijn goede argumenten voor de veronderstelling, dat deze verschillen genetisch bepaald zijn. De belangrijkste vormen van resistentie zijn „totale resistentie", die zijn invloed doet

FIG. 44.2.a Log-i diagram. Field observations: Heines VII/Noordoostpolder/7013, 7014, 7016, 7017 and 7018. Trial observations: 1960 detailed experiment at Wageningen.
LMI = leaf mass index
RMI = rust mass index



gelden in alle delen van de plant, en „volwassen-plantresistentie", die zijn invloed alleen doet gelden in halmbladeren, stengel en aar; totale resistentie en volwassen-plantresistentie zijn fysio-specifiek. Het beeld wordt gecompliceerd, doordat „hitteresistentie" gesuperponeerd kan worden over andere vormen van resistentie. Zonder kruisingsproeven te verrichten is reeds een oriënterend genetisch onderzoek van de resistentie mogelijk met behulp van de PERSON-analyse (25.2). Een aantal genen voor totale resistentie en voor volwassen-plantresistentie wordt onderscheiden: een dergelijke analyse is zonder bevestiging door kruisingsproeven van sterk speculatieve aard. Getracht wordt een niet-fysio-specifieke vorm van resistentie te omschrijven (25.3).

3 Qualitatieve epidemiologie

32 De incubatietijd is bestudeerd met behulp van veldproeven, waarvoor de combinatie Heines VII – fysio W12 werd gebruikt (32,1,2). De incubatietijd blijkt sterk te variëren, van 11 tot 118 dagen, al naar gelang de temperatuur. Het verband tussen de incubatietijd en de temperatuur is vastgesteld in een aantal figuren (32.2a, b, c, d), waaronder een figuur van een rekenlineaal, dienende om van ieder willekeurig tijdsbestek het „potentieel aantal roestgeneraties" n_g te schatten. Het potentiële aantal roestgeneraties per jaar N_g = c. 17. Bij het inoculeren van een groot aantal bladeren tegelijkertijd blijkt er een toevalsvariatie in de lengte der incubatietijd te zijn, die niet zozeer aan de temperatuur als aan kleine verschillen in infectie-omstandigheden en in vatbaarheid der verschillende blaadjes moet worden toegeschreven (32.3). Het inoculatie-resultaat is in de zomer veel gunstiger dan in de winter (32.4, fig. 32.4).

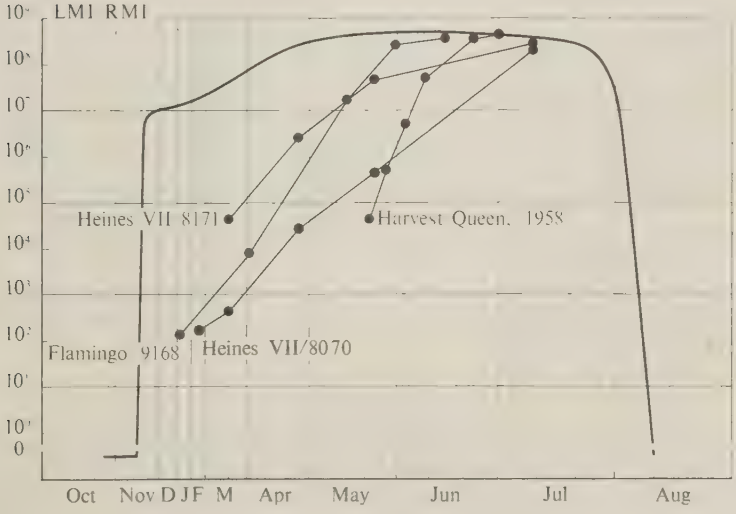
33, 35 Gele roest overwintert op het normale gewas en op opslag (33). In de winter is de roest heel moeilijk te vinden in verband met de lange incubatietijd en de korte sporulatietijd (37.1). Overzomering vindt plaats via knipaartjes, opslag van voor het maaien, doorwas en opslag van na het maaien (35). Zelfs in de zeer droge zomer van 1959 werd deze cyclus waargenomen. 's Nachts is meestal voldoende dauw aanwezig om infectie mogelijk te maken en ook in droge zomers kan haardvorming op opslag optreden. Een overzomeringscyclus in de Alpen is mogelijk, omdat daar tengevolge van de grote hoogte oogst- en zaaitijd kunnen overlappen. Transport van inoculum naar grote hoogte is bewezen (35.3), transport van inoculum van laat rijpende tarwe op grote hoogte naar opslag in de dalen wordt mogelijk geacht.

34 Haardvorming is in detail bestudeerd. In een proef met een kunstmatige haard zijn een aantal sporulatiegolven vastgesteld. Tot vier golven zijn waarneembaar, maar de derde en de vierde sporulatiegolf vloeien al geleidelijk ineen tot een continue toename van het aantal sporulerende blaadjes (fig. 34.2). In de praktijk is haardvorming zeer frequent; afhankelijk van het weer blijven de haarden gelocaliseerd of zij breiden zich snel uit tot een ernstige aantasting. Als ene uiterste van de roestontwikkeling geldt de focale epidemie, waarbij de haardvorming sterk op de voorgrond treedt; het andere uiterste is de generale epidemie, die ontstaat wanneer in de herfst al veel inoculum voorradig is. De gewone gang van zaken ligt veelal tussen deze beide uitersten in en vaak ziet men, dat een focale epidemie geleidelijk generaliseert (34.4). Locale verschillen in aantasting treden veelvuldig op; deze worden toegeschreven aan verschillen in mikroklimaat, die het wel of niet tot stand komen van een infectie be-

palen wanneer de weersomstandigheden „marginaal" zijn. Dergelijke kleine verschillen in mikroklimaat kunnen berusten op verschillen in zaaitijd, bemesting, bodemstructuur of expositie ten opzichte van de wind en de zon (34.3). Als het weer over langere tijd gunstig is geweest voor verspreiding en infectie van de gele roest, dan zijn verschillen in bemesting en bodemstructuur van geen betekenis. Onder zulke omstandigheden vallen de variaties tussen de normale practijkpercelen ruim binnen de tolerantiegrenzen van de roest (34.5). Nederland en Zwitserland zijn centra waar de roestendemie een hoge intensiteit bezit. Ook in andere landen is de gele roest endemisch, maar de intensiteit van de endemie is daar veelal zeer gering. Kruisinfectie tussen de verschillende centra is van weinig practisch belang in verband met de grote regionale spreiding van het rassensortiment en de vergaande fysiologische specialisatie van de roest (34.6).

36 Sporenverspreiding over korte afstanden (tientallen meters) is onder vrijwel alle omstandigheden mogelijk, maar vindt vooral plaats in herfst en voorjaar. Transport over middelgrote afstanden (kilometers) is bewezen in de Noordoostpolder, in Oostelijk Flevoland en in Zwitserland; afstanden van 1.8 tot 18 kilometer werden genoteerd. Verspreiding over lange afstanden (honderden kilometers) is eveneens mogelijk. Uit de literatuur zijn afstanden tot 1.000 km (in één sprong) en 2.400 km (met tussenstappen) bekend. Er zijn goede argumenten om in Europa ook te rekenen met verspreiding over afstanden tot 800 km (kaart 36.3). In verband met de grote variatie van rassen in Noord-west Europa is het gevaar van een dergelijke lange-afstandsverspreiding in de regel

FIG. 44.2.b Log-i diagram. Field observations: Heines VII/Haarlemmermeerpolder/8070, 8171 and Flamingo/Noordoostpolder/9168. Trial observations: International Yellow Rust Trial at Rilland-Bath, 1958, Harvest Queen.
LMI = leaf mass index
RMI = rust mass index



gering te achten; gevaar dreigt slechts bij de meer universele rassen als Cappelle en Heines VII, die in vele landen van Europa verbouwd worden.

37 Er zijn een aantal weertypen, die een duidelijke invloed op de roest te zien geven. Bij koude neemt de incubatietijd toe, bij strenge vorst kan de roest met zijn gastheer doodvriezen. Een sterke afwisseling van sneeuw en regen, van vriezen en opdooien tegen het einde van de winter drukt de roestpopulatie, die zich dan vooral bevindt in de onderste en oudste blaadjes. Deze hebben na de winter weinig weerstandsvermogen, zij vriezen snel dood of worden door de regen tegen de grond geslagen waarna zij wegrotten. In het vroege voorjaar treedt dikwijls een lange droogteperiode op, die de roestverspreiding remt; in deze periode is de haardvorming soms zeer markant. Zware regen in het voorjaar kan de sporulerenden bladeren tegen de grond slaan en met slijk bedekken; de roest is dan verloren voor de voortplanting. Hitteperioden in juni en juli remmen de opmars van de roest, zonder dat de roestpopulatie als geheel gedood wordt.

38, 39 Na een bespreking van enkele literatuurgegevens (38), worden in een laatste analyse van de Heines VII-epidemieën nogmaals de factoren N_g, n_g, zomerregenval en tarwe-areaal in verband gebracht met de intensiteit van de epidemieën.

4 Quantitatieve epidemiologie

41 De termen „bladmassa" en „roestmassa", en „blad massa index" en „roest massa index", worden geïntroduceerd ter quantitatieve beschrijving van de tarwe- en roestpopulatie. Om het verloop van een roestaantasting grafisch voor te stellen zijn vier typen van diagrammen op hun merites getoetst, te weten: het logit-lineair diagram, het log-linear diagram, het log-i diagram en het logit-i diagram.

43, 44 In de log-diagrammen kunnen de tarwe- en de roestontwikkeling in hun onderling verband worden weergegeven; het gebruik van de i-tijdschaal ondervangt het bezwaar van de variabele incubatietijd. De verkregen ontwikkelingscurven zijn gebogen lijnen, die zich slecht lenen tot nader onderzoek.

42, 44 In de logit-diagrammen wordt alleen de roestontwikkeling weergegeven. In een logit-diagram liggen de opeenvolgende waarnemingen aan een zeer vatbaar object redelijkerwijs op een rechte lijn. Bij veldwaarnemingen moet daartoe de lineaire tijdschaal door de i-tijdschaal vervangen worden. Een aantal toevallige en systematische afwijkingen van de rechte lijn wordt besproken.

45 Het logit-diagram vindt een toepassing in de „roestdrukwaarde"; de roestdrukwaarde voor verschillende plaatsen in Europa in het jaar 1957 is in kaart gebracht (kaart 45).

46 De verwachting wordt uitgesproken en toegelicht, dat het gebruik van logit-i diagrammen mede zal leiden tot een beter inzicht in het samenspel van gastheer, parasiet en milieu.

Acknowledgments

Many thanks are due to the Board of the Netherlands Grain-Centre for organizing and financing this research; to Dr. ten Houten, Director of the Institute of Phytopathological Research (I.P.O.), for putting the knowledge and

the equipment of the I.P.O. at the writer's disposal; to Professor OORT for hospitality at the Laboratory of Phytopathology and for guidance in the course of the work; to Dr. S'JACOB, Head of the Resistance Department of the I.P.O., for his friendly co-operation.

The kindness of Professor HASSEBRAUK, Director of the *Institut für Botanik* of the *Biologische Bundesanstalt* at Braunschweig (Germany), and of Dr. EVA FUCHS, charged with the yellow rust identification work at Braunschweig, are remembered with gratitude.

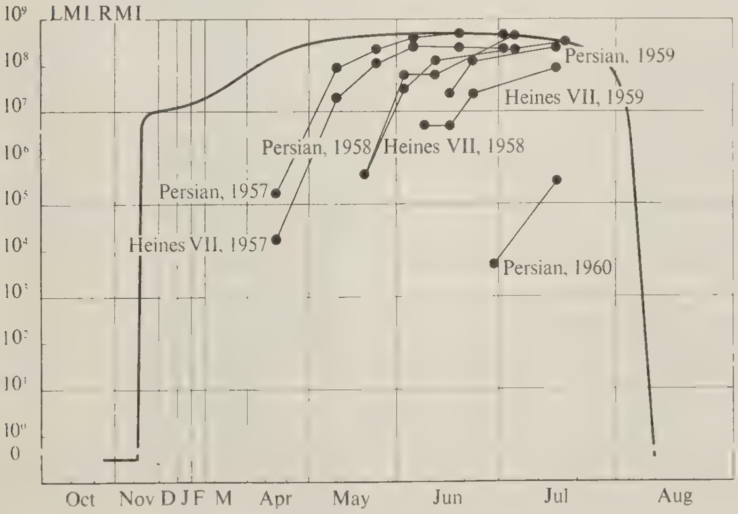
Some 150 trial observers all over Europe offered their help in a most co-operative way.

Special mention deserve the Agricultural Advisory Service (RLVD), the Plant Protection Service (PD) and the Zuiderzee Polders Development and Colonization Authority *(Directie van de Wieringermeer)* for their invaluable help in rust observation work and experimentation. The Foundation for Agricultural Plant Breeding (SVP), where Dr. DANTUMA was always prepared to give advice and help, the Royal Netherlands Metereological Institute (KNMI) and the Institute for Research on Varieties of Field Crops (IVRO) are warmly thanked for their interest and informations.

Mrs. DAENDELS-WILSON most kindly corrected the English and gave many valuable suggestions.

Special thanks are due to the technicians HOOGKAMER and BASSET, who most loyally assisted in the research work and who never feared new tasks.

FIG. 44.2.c Observations from International Yellow Rust Trial 3510 at Wieringerwerf over the years 1957–60: Heines VII and Persian; compare fig. 42.5.
LMI = leaf mass index
RMI = rust mass index



7 APPENDIX

In the text the appendix tables are referred to by the letter A, e.g.: (table A.24.42.c).

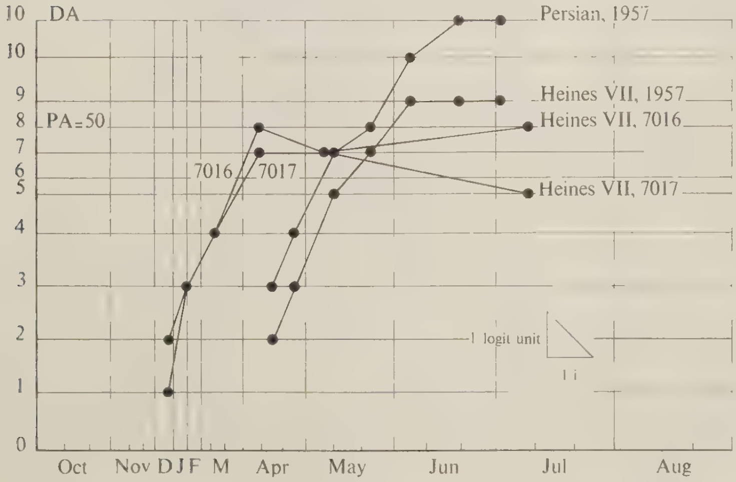
TABLE A.11.3 List of International Yellow Rust Trials. Names of countries are written in English, other geographical names are written in the respective national languages. For details see ZADOKS, 1958, 1959a, 1960b.

NORWAY	
0110	Vollebekk
0120	Hamar
0130	Åmot
0140	Sarpsborg
SWEDEN	
0410	Svalöf
0420	Landskrona
DENMARK	
1110	Grønning
1120	Ødum
1130	Horsens
1210	Børkop
1220	Askov
1230	Esbjerg
1310	Aarslev
1410	København
1420	Tystofte
1510	Abed
1610	Aakirkeby
GERMANY	
2110	Waterneverstorf
2120	Siek
2210	Ohlendorf
2220	Upleward
2230	Carolinensiel
2240	Schnega
2250-4	Braunschweig-Gliesmarode
2260	Schöningen
2270	Schladen
2280	Domäne Voldagsen über Kreiensen
2290	Einbeck
2310	Köln-Vogelsang
2320	Albersloh
2410	Giessen
2510	Monsheim
2610	Stuttgart-Hohenheim
2620	Stuttgart-Karlshof
2630	Reutlingen
2710	Seligenstadt
2720	Marktredwitz
2730	Irlbach
2740	Weihenstephan/Freising
2750	Feldkirchen
2760	Landsberg/Lech
2810	Gross-Lüsewitz
2821-2	Hohenthurm bei Halle
2830	Halle-Stichelsdorf
2840	Dornburg am Saale
2850	Hadmersleben
POLAND	
2910	Warszawa
NETHERLANDS	
3210	Westpolder
3220	Nieuw-Beerta
3230	Ferwerd
3240	Sint Anna Parochie
3250	Oudemirdum
3260	Roodeschool
3270	Nieuwe Bildtdijk
3280	Haren
3310	Wieringerwaard
3320	Beemster
3330	IJpolder
3340	Hoofddorp
3350	Bleiswijk
3360	Westmaas
3400	Middelharnis
3410	Dinteloord
3420	Tholen
3430	Bruinisse
3440	Noord-Beveland
3450	Wilhelminadorp
3451	Oudelande
3460	Rilland-Bath
3470	Walcheren
3480	IJzendijke
3490	Hulst
3500	Breezand
3510	Wieringerwerf
3520	Emmeloord
3530	D 22 (N.O.P.)
3540	Marknesse
3550	Ketelhaven
3560	Lelystad
3570	Knarhaven
3610	Werkendam
3620	Wageningen
3630	Wageningen
3640	Randwijk
3650	Andelst
3671-9	Baarn
3710	Borgercompagnie
3720	Emmercompascuum
3730	Norg
3740	Rolde
3810	Dongen

TABLE A.11.3 Continued

3820	Maarheeze
3830	Asten
3840	Ottersum
3910	Beesel
3920	Wijnandsrade
BELGIUM	
4110	Oostkerke bij Diksmuide
4120	Lemberge
4130	Roeselare
4150	Wulpen
4160	Aalbeke
4210	Poppel
4220	Herentals
4230	Stabroek
4310	Leuven-Heverlee
4320	Gembloux
LUXEMBURG	
4910	Ettelbrück
4920	Luxemburg
GREAT BRITAIN	
5110	Edinburgh/Boghall
5120	Auchincruive
5210	Winmarleigh/Preston
5220	Chester
5310	Cockle Park near Newcastle
5320	Headly Hall near Tadcaster
5410	Cambridge, N.I.A.B.
5420	Cambridge, P.B.I.
5430	Sprowston
5440	Sutton Bonington
5450	Grimsby
5510	Newport
5520	Stourbridge
5530	Sunninghill
5610	Trawscoed (Cardiganshire)
5620	Plas Gogerddan
5710	Rosemaund (Hereford)
7520	Seale-Hayne
5810	Wye (Kent)
5820	Sparsholt
5830	Southampton
5910	Loughgall
IRELAND	
6110	Backweston Departments Farm (Kildare)

FIG. 44.3.a Logit-i diagram. Field observations: Heines VII/Noordoostpolder/7016, 7017. Trial observations: International Yellow Rust Trial 3510 at Wieringerwerf (Netherlands), 1957, Persian and Heines VII. The earlier observations fit fairly well to straight lines which are approximately parallel; the later observations deviate from the expected straight lines.
DA = degree of attack, plotted on a logistic scale
i = incubation time
PA = percentage of attack



6210	Johnstown/Wexford
6310	Midleton
FRANCE	
7010	Cappelle par Templeuve (Nord)
7020	Auchy-lez-Orchies (Nord)
7110	Estrées-St-Denis (Oise)
7120	Versailles (S. et O.)
7130	Grignon (S. et O.)
7140	Montfort l'Amaury (S. et O.)
7150	Coulommiers (S. et M.)
7160	Reims
7210	Le Neubourg (Eure)
7220	Rennes (Ille et Vilaine)
7310	Blois (Loir et Cher)
7320	Périgueux (Dordogne)
7410	Chatillon s. Seine (Côte d'Or)
7420	Dijon (Côte d'Or)
7610	Clermont-Ferrand (Puy-de-Dôme)
7620	Rodez (Aveyron)
7710	Montpellier (Hérault)
7720	Valence s. Rhône (Drôme)
7910	Ondes (Haute Garonne)
SWITZERLAND	
8110	Cery près Lausanne (Vaud)
8120	La Frêtaz (Vaud)
8130	Illarsaz
8210	Wallestalden (Bern)
8310	Reckenholz
8410	Haag-Gams
8530	Realta (Graubünden)
8540	Maran bei Arosa (Graubünden)
EGYPT	
9011	Cairo
KENYA	
9021	Molo
9031	Kenya
AUSTRIA	
9120	Reichersberg (Oberösterreich)
9150	Petzenkirchen (Niederösterreich)
9160	Fuchsenbigl
9170	Drauhofen (Kärnten)
9180	Sankt Donat (Kärnten)
YUGOSLAVIA	
9220	Zagreb
9250	Novi Sad
ITALY	
9310	Bergamo
9320	Lonigo
9330	Bologna
9350	Firenze (Cascine)
9360	Firenze
9370	Roma
9380	Foggia
TURKEY	
9410	Ankara 1
9420	Ankara 2
SPAIN	
9510	Zaragoza
9520	Madrid
GREECE	
9610	Thessaloniki
9620	Halkidikis
9630	Kilkis
PORTUGAL	
9730	Oeiras
9750	Elvas
ISRAEL	
9910	Hof Asdod
9920	Rehovot

TABLE A.24.26 Table for the transformation of DA into RPA

DA \ IL	6	7	8	9	10
0	0	0	0	0	0
1	0	0	0	0	0
2	0	0	0	0	0
3	1	0	0	0	0
4	10	4	2	1	1
5	50	20	10	7	5
6	100	40	20	13	10
7	.	100	50	33	25
8	.	.	100	67	50
9	.	.	.	100	75
10	.	.	.	.	100

entries: relative percentage of attack RPA

FIG. 44.3.b Logit-i diagram. Field observations: Heines VII/Haarlemmermeerpolder/8070, 8171 and Flamingo/Noordoostpolder/9168; trial observations: International Yellow Rust Trial 3460 at Rilland-Bath (Netherlands), 1957, Harvest Queen. The observations fit fairly well to the expected straight lines. The slopes of the logit lines of the field observations differ considerably from those in fig. 44.2.a.
DA = degree of attack, plotted on a logistic scale
i = incubation time
PA = percentage of attack
N.B.: Erroneously, the line for DA = 1 has been drawn c. 3 mm. too low.

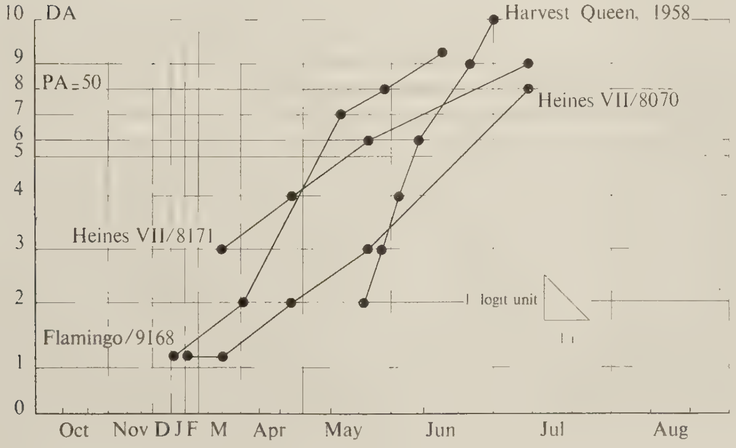


TABLE A.23.5 Varieties tested in the greenhouse in 1959 and 1960; infection types on primary leaves

greenhouse number	race-Wageningen key	W4	W	6				W8		
	race-Braunschweig key	B1x	B	·				B 2x/55		
	number of isolate	119	9789*a*	8894	117	118	8097	8125	8876	8881
1	Michigan Amber	4	4	i+4	4	4	4	4	4	4
2	Blé Rouge d'Ecosse	0	3	4	2^{+}	4^{-}	3	2	2—4	2—4
3	Strubes Dickkopf	0	2	4	4	4^{-}	3	3	2—4	2—4
4	Webster	4	2^{-}	0—4	4	2	2	1—2	0—4	0—4
5	Holzapfels Frühweizen	0—2	4	4^{-}	0—4	0+4	$2^{\pm}$	0—4	2—4	0—4
6	Vilmorin 23	0—4	4^{-}	i+4	4	4	4^{-}	4	4	4
7	Heines Kolben	4	0	i—0^{+}	0	0^{+}	0—1	0—1	0	0—1
8	Carstens V	0	4	4^{-}	0	0	0—1	0—1	0^{+}	0—2
9	Spaldings Prolific	0	0^{+}	i^{+}	i—0	i—0	0—1	0—1	2—4	2—4
10	Chinese 166	0	0	i—0	0	0	i	i	i	0
11	Rouge prolifique barbu	0	0	i—2	0	0	1^{-}	1—2	2—4	2—4
12	Heines VII	0—4	0	0^{+}	0	0^{+}	2^{+}	i^{+}	i	i
13	Cappelle	0	0	i^{+}	0^{+}	0^{+}	4	4	4	4
14	Vilmorin 27	i—2	1—2	i+4^{-}	4	2—4	2—4	4	4	4
15	Frontana	4	2	2—4	0—1	1—2	0—1	1	i	2—4
16	Riebesel 51–52	0	0	i	0	0	i	i	i	i
17	Peko	4^{-}	0	i	0	0	0	$0^{\pm}$	i	0^{+}
18	Panter	0	0	i—2	0	0	1—2	1	2—4	2—4
19	Hybrid 46	i+4	0—1	i+4	0+4	0—4	0—4	0+4	i+4	0+4
20	Leda	0+4	2	4	4	3	4	4	4	0—1
21	Alba	0^{+}	0	4	4	2—4	2	2	3^{-}	0—1
22	Reichersberg 42	$0^{\pm}$	0	0	0	0	1	1	·	·
24	Ile de France	4^{-}	$2^{\pm}$	4^{-}	4^{-}	4	2	2^{+}	·	·
25	Staring	4	0	4	4	4	4	4	·	·
26	Funo	i	0	i^{+}	0	0	0	2^{-}	·	·
27	Mado	4	0^{+}	i+4	4	4	2	3	·	·
28	Minister	i+4	0	i	0	0—1	4	2	·	·
29	Felix	i	0	2—4	0	0	0+4	4	·	·
30	Selkirk	2^{+}	2	2—4	2	2	2	1	·	·
31	Heines 110	i	0	i	0	0	i	i	i	i
32	Rubis	4	·	$0^{\pm}$	2	2^{-}	·	·	·	·
33	Probus	4	·	4	2—4	4^{-}	·	·	·	·
34	Nord	0+4	·	i—4	2—4	2^{-}	·	·	·	·
35	Triumph	4	·	4	4^{-}	4	·	·	·	·
36	Blé des Dômes	i+4	·	0	0^{+}	0	·	·	·	·
37	Merlin	i+4	·	i—2	0	0	·	·	·	·
38	Halle 3435/46	i	·	i—0	0	0	·	·	·	·
39	Medsched × Ridit	0	·	i+4	0^{+}	0^{+}	·	·	·	·
40	Bonus	i+4	·	i—2	0—2	0	·	·	·	·
41	Harvest Queen	4	·	4	4	4	·	·	·	·
42	Etoile de Choisy	4	·	4	4	4	·	·	·	·
43	Marne	i+2	·	i—4	2—4	2—4	·	·	·	·
44	Carest	i+4	·	i—4	4	2—4	·	·	·	·
45	Persian	4	·	i+4	4	4^{-}	·	·	·	·
46	Heines IV	4	·	i+4	4	4	·	·	·	·
47	Flamingo	i	·	i+4	0	0	·	·	·	·
48	Stella	i+4	·	i	0	0^{+}	·	·	·	·
49	Little Club	i+4	·	i—4	2—4	2—4	·	·	·	·
50	Hope × Timstein	i	·	0	0	0	·	·	·	·
51	Redman	i+4	·	4	4	4	·	·	·	·
52	Carpo	i+4	·	4	2	4	·	·	·	·
53	Triticum spelta album	i	·	i	0	i—0	·	·	·	·
54	T. dicoccum tricoccum	4	·	4	4	4	·	·	·	·

				W 12								
				B 54								
9-345*c*	9-345*d*	9547	9-714*a*	inc.	8147	8700	8861	8880	8887	9168	9793	greenhouse number
4	4	4	4	4	4	4	4	4	4	4	4	1
0	4	4	4	4	3	4	2—4	2—4	2—4	4	0—4	2
3	i—2	4	4	4	4^-	4	4^-	4	2—4	4	2—4	3
2^-	3—4	2—4	1—4	0^+	$1^\pm$	0—4	0—2	1^+	1^+	2^+	1	4
0—4	1—2	2—4	1—4	1—4	0—4	4	2—4	2—4	0—4	4	0—4	5
4^-	4	4^-	4	0	1—3	i—1	0	0	0	0	0	6
0	0^+	0	0	4	4^-	4	4	4	2—4	4	4	7
0—1	i^-	1	i—4	0	1—2	0—4	0—1	0—2	$1^\pm$	0	0	8
0	0—2	1	i+2	0^+	i—2	0—4	0^+	0—4	0—2	i—1	0	9
0	i	0	i	0	i	0	i	0	0	0	0	10
$0^\pm$	4	2	i+4	0	2—3	0—4	2—4	0—4	0—1	0—2	0	11
0	0	0	0	4	4	4	4^-	0—4	4	4	0—4	12
0	1—4	1—4	0—4	0	$0^\pm$	0	0	0	0	0	0	13
2—4	i—4	$0—4^-$	0—4	0	1	0—2	2	0—1	2	0	0	14
1—3	i	0—4	4	3—4	4	4	4	4	4	4^-	4	15
0	i	0	i	0	i	0	i	i	i	0	.	16
0	i	0	i	2^+	4	4	4	i	4^-	4	.	17
0	i	0^+	i—4	0	2	1	2	2—4	1	0—4	.	18
0+4	4	0+4	i+4	0	$0^\pm$	0	1	1—4	1—2	i	0	19
4	$1^\pm$	2	i+2	0—4	4	4	4	4	4	4	0	20
4	1	2	i	.	4	2—4	$2^\pm$	4	4^-	4	0	21
0	$2^\pm$	0	i^+	0	0	1	1	0	0	0	0	22
2+4	4	1—4	i+4	0^+	0	2—4	2	2	0—4	$1^\pm$	0	24
2	4	0—4	i+4	0	i	0	2	0	2	i	0	25
0	0	0	0—4	0	i	0	0—2	0—2	$1^\pm$	0	.	26
2	i+4	0—4	i^+	0	i	0	0	1	2	2	0	27
0	i—4	0^+	$1^\pm$	0	i	0	0	0—4	1	0	0	28
0	4	0—4	i+4	0	i	0	0—2	4	1(+4)	i	0	29
2	4	0—4	2	1^+	0	1	0	2^+	1	2	2	30
0	i	0	i	0	i	i	i	i	0	i	.	31
.	i	0	$1^\pm$	.	.	4	.	4	4	i+4	.	32
.	4^-	0—4	4	.	.	4	.	4	4^-	i+4	.	33
.	4	4	4	.	.	i	.	0	i	i	.	34
.	4	4	4	.	.	i+4	.	4	4^-	$i+4^-$	.	35
.	i—0	0	$0^\pm$	.	.	i+4	.	0—4	4	$i+4^-$	.	36
.	i—2	0	i+4	.	.	i+4	.	$1^\pm$	4	i	.	37
.	i^+	0	i	.	.	i	.	0(+4)	i	i	.	38
.	i^+	0—2	i+4	.	.	i+4	.	4	i+4	i+4	.	39
.	i^+	0	0	.	.	i+2	.	2—4	i+4	i+4	.	40
.	4	4	4	.	.	4	.	4	4	i+4	.	41
.	4	4	4	.	.	4	.	4	4	$i+4^-$	.	42
.	4	4	4	.	.	2	.	$1^\pm$	1—4	i+4	.	43
.	4	4	4	.	.	2	.	0^+	4	$i+4^-$	.	44
.	4	4	4	.	.	i+4	.	4	4	i+4	.	45
.	4	0—2	4	.	.	i+4	.	4	4	4	.	46
.	i	0	i+4	.	.	4	.	0(+4)	4^-	4	.	47
.	i	0^+	i—2	.	.	0—4	.	0—2	2—4	i—4	.	48
.	i+4	0—4	i+4	.	.	4	.	4	4	4	.	49
.	$i^\pm$	0	2	.	.	0	.	2	0	i	.	50
.	4	4	4	.	.	4	.	4	4	i—4	.	51
.	i+4	4^-	4	.	.	4	.	4^-	4	4	.	52
.	i	0	i	.	.	0	.	0	i	i	.	53
.	4	4	4	.	.	4	.	4	4	4	.	54

Table A.23.5 (continued)

greenhouse number	race-Wageningen key	W 13			W 14						W
	race-Braunschweig key	B 27/53			B7xV$_1$	B 17/26					B
	number of isolate	105	113	9812	115	116	8130*b*	8153	8589	8600	889
1	Michigan Amber	4	4	4	4	4	4	4	4	4	4
2	Blé Rouge d'Ecosse	2—4	4	4	4	2—4	4	2—3	4	4	4
3	Strubes Dickkopf	2	4	$1^{\pm}$	2^{-}	0—4	4	2	4	0^{+}	4
4	Webster	$2^{\pm}$	1—2	0—4	2	0—2	2	0^{+}	0—4	2	0
5	Holzapfels Frühweizen	2—4	4	4	2—4	4	2—4	$2^{\pm}$	4	0—4	2—4
6	Vilmorin 23	0	0^{+}	0	0	0	0—1	0—1	0	0	0
7	Heines Kolben	0	0	0	0	0	0—1	0—1	$2^{\pm}$	0—1	0
8	Carstens V	4	4	4	4	4	0—2	0—1	$2^{\pm}$	0	1
9	Spaldings Prolific	0—2	1—4	1—2	2—4	0—2	$1^{\pm}$	i—2	0—2	0—4	0
10	Chinese 166	4	4	4	0	0	0	i	i—0	0	0
11	Rouge prolifique barbu	0^{+}	2	0	2	0	1—4	i—1	0—4	0—4	0—2
12	Heines VII	0^{+}	2	0	0—2	0	4^{-}	2	4	0—4	0
13	Cappelle	0	0	0	0	0	0	0	0	0	0
14	Vilmorin 27	0	0—1	0	0	0	1—2	$1^{\pm}$	0—4	0	0
15	Frontana	0—2^{-}	2^{-}—4	2—4	0—2	$1^{\pm}$	0—2	0—4	0—4	0+4	1
16	Riebesel 51-52	0	0	0	0	0	0	i	i	i—0	0
17	Peko	0	0	0	0	0	0	$1^{\pm}$	0	0^{+}	0
18	Panter	0	0—4	0	0	0	0—2	i	1	0^{+}	0—2
19	Hybrid 46	0—1	1—4	0—2	0	$0^{\pm}$	0	i	0	0—4	0—1
20	Leda	2	4	2+4	3	0+2	4	4	4	0—1	4
21	Alba	1	$2^{\pm}$	0—2	2—3	0	4	$2^{\pm}$	4^{-}	1	4
22	Reichersberg 42	0	1	2^{-}	0	0	1	1	0	0	0
24	Ile de France	$2^{\pm}$	1+4	0+2	0	0	2^{+}	4	2—4	0	2
25	Staring	0	0	0	0	0	2	4	0	0	0
26	Funo	0	0	0	–	0	0	2	0—4	0	0
27	Mado	0	0—2	$0^{\pm}$	0	0+2	2	2	2	0	1
28	Minister	0	i—2	0	0	0	$1^{\pm}$	2	2	0	0
29	Felix	$1^{\pm}$	0	0+4	0	0	2	$2^{\pm}$	2	0	0
30	Selkirk	2	4^{-}	2—4	3	2	2	0	i—4^{-}	1	1—2
31	Heines 110	0—1	0—1	0	0	0	i	i	i—0	i	i
32	Rubis	$2^{\pm}$	2—4	$2^{\pm}$	2	0—2	.	.	4	4^{-}	1—2
33	Probus	4	4	4	4	4	.	.	i—4	4	4
34	Nord	0	0^{+}	0	0	0	.	.	i	0	0
35	Triumph	i+3	3—4	4	0^{+}	2+4	.	.	i—4	2—4	4
36	Blé des Dômes	2	2	0—2	0—2	0—2	.	.	4	4	0—2
37	Merlin	0^{+}	0—1	0^{+}	0	0—1	.	.	4	4	1—2
38	Halle 3435/46	2	4	4	0	0	.	.	i	0	0
39	Medsched × Ridit	0+2	0 (+4)	0—4	0^{+}	0—4	.	.	i—4	0+4	2
40	Bonus	1	2	1—2	1	2	.	.	i	$0^{\pm}$	1—2
41	Harvest Queen	4	4	4	4	4	.	.	4	4	4
42	Etoile de Choisy	2—3	4	4	3	4	.	.	4	4	2—4
43	Marne	0	1^{+}	0—2	0^{+}	0—2	.	.	i—4	1—4	2
44	Carest	0	1—2	0^{+}	$1^{\pm}$	0—1	.	.	4^{-}	2	2
45	Persian	2—3	4	4	2^{+}	2^{+}	.	.	4	4^{-}	4
46	Heines IV	4	4	4	3	4	.	.	4	4	4
47	Flamingo	0	$1^{\pm}$	i—0	0	0	.	.	i—4	0—4	0
48	Stella	0	0—1	0	0	0	0	.	2	2^{-}	0—1
49	Little Club	2—4	2—4	4^{-}	2	i—4	4	.	4	3—4	4
50	Hope × Timstein	0	0—1	0	0—2	0	.	.	0	0	0
51	Redman	4	4	4	4	4	4	.	4	4	4
52	Carpo	0	2	i+4	2	2	4	.	4^{-}	1—2	2
53	Triticum spelta album	0	0	i	0	0	0	.	i	0	0
54	T. dicoccum tricoccum	4	4	4	4	4	.	.	4	4	4

9775	9791*b*	9792	9798	9802	W 4 B 1x	W 6 .	W 8 B 2x/55	W 12 B 54	W 13 B 27/53	W 14 B 6/7/ 7xV_1	W 16 B .	greenhouse number
4	4	4	4	4	4	4	4	4	4	4	4	1
i—3	4	4	4	0—4	0	3	0 -4	0—4	4	2—4	4	2
i—3	4^{-}	4	i—4	4	0	2	2—4	2—4	1—4	0—4	0 4	3
0^{+}	0^{+}	$2^{\pm}$	2^{-}	1	4	$2^{\pm}$	0—4	0—2	0—4	0—2	0 2	4
0—1	0 -4	2	i—4	0—1	0—2	4	0—4	0—4	4	2—4	0—4	5
0	0	i	i	0	0—4	4^{-}	4	0^{-}	0	0	0^{+}	6
0	$2^{\pm}$	0	i—0	$2^{\pm}$	4	0	0	4	0	0	0^{+}	7
0	0—2	0	i—1	0^{+}	0	4	0^{+}	0^{+}	4	4	0^{+}	8
0^{+}	0—2	0—4	i—3	0+4	0	0^{+}	0—4	0—4	0—4	0—4	0—2	9
0	0	0	0	0	0	0	0	i—0	4^{-}	0	i—0	10
0—1	0	i	1—2	0	0	0	0—4	0 —4	0—2	0—2	0—4	11
0	4	i—2	i	4^{-}	0—4	0	0^{+}	4	0—2	0—2	0—4	12
0	0	i	0	0	0	0	0—4	0	0	0	0	13
0	0	0	i—0	0	i—2	1—4	2—4	0^{+}	0	0	0^{+}	14
0	0—2	0	0—4	2^{-}	4	2^{+}	0—4	4	0—4	0—2	0—4	15
0	i	0	i	0	0	0	i—0	i—0	0	0	i—0	16
i—0	i—4	0	0	0	4^{-}	0	0	i—4	0	0	0^{+}	17
0	0	0	0	0	0	0	0—4	0—4	0—4	0	0—2	18
0—4	i—0	0^{+}	0+4	0	i+4	0—4	0+4	0—4	0—4	0	0+4	19
$2^{\pm}$	4	4	4	2	0+4	2—4	2—4	0—4	2—4	0—3	0—4	20
0	4	4	$0+4^{-}$	2	0^{+}	0—4	0—4	0—4	0—2	0—3	0 —4	21
0	0	0^{+}	i	0	$0^{\pm}$	0	0—1	0	0—2	0	0	22
0	0	i—4	i+4	i^{+}	4^{-}	2^{+}	2—4	0—4	0—2	0	0—4	24
0	0	0—2	i—4	0	4	0—4	4^{-}	0—2	0	0	0—4	25
0	0	0	i	i	i	0	0^{+}	0—2	0	0	0	26
0	0—1	4^{-}	i+4	i—2	4	0—4	0—4	0—2	0^{+}	0—2	0—4	27
0	0	i	i	i	i+4	0	0—4	0^{+}	0	0	0—2	28
0	0	i	i	i	i	0—4	0+4	0—4	0—4	0	0—2	29
0	0	2—3	2	2	2^{+}	2—4	$2^{\pm}$	0—2	2—4	2—3	0—2	30
0	i	0	i	0	i	0	i—0	i—0	0	0	0	31
0—2	0—4	1—4	i	4	4	0	0—2	4	2—4	0—2	0—4	32
4	4	4	4	4	4	4	4^{-}	4	4	4	4	33
0	0	0	i	i—0	0+4	i—4	2—4	i	0	0	0	34
4	0	4	i	4	4	4	4	i+4	3—4	0—4	0—4	35
0^{+}	2	0	i—2	4	i+4	0	0	4	2	0—2	0—4	36
0^{+}	2	0—2	i	4	i+4	i—2	0	i—4	0	0—1	0—4	37
0	0	0	i	i	i	i—0	0	i	4^{-}	0	0	38
0^{+}	i—3	0+4	i+4	i	0	i+4	0	i+4	0—4	0—4	0—4	39
0	0	i—4	i—2	i—2	i+4	i—2	0	i+4	1—2	1—2	0—4	40
4	3	i—4	4	4	4	4	4	4	4	4	4	41
i—4	2—3	4	4	4	4	4	4	4	4	3—4	2—4	42
0	1	i—2	$0^{\pm}$	0—2	i+2	i—4	2—4	1—4	0 —2	0 —2	0—2	43
0—2	2	2	i+4	4	i+4	i—4	3—4	4	0—2	$1^{\pm}$	0—4	44
4	4	4	i+4	4	4	i+4	4	4	4^{-}	2^{+}	4	45
4	4	4	i+4	4	4	i+4	4	4	4	3—4	4	46
i—0	i—4	i—4	i	0—2	i	i+4	0 —4	0+4	0—1	0	0 -4	47
0	i—4	0	i	0—2	i+4	i	0^{+}	0—4	0—1	0	0—4	48
0—4	4	4	4	4	i+4	i—4	0—4	4	2—4	2—4	0 -4	49
0	0	0	i	0	i	0	0	0^{+}	0^{+}	0—2	0	50
4	4	4	i—4	4	i+4	4	4	4	4	4	4	51
0^{+}	4	4	i—4	1	i+4	4	2—4	4	0—4	2	0—4	52
0	i	0	0	i	i	i	0	0	i—0	0	0	53
4	4	4	4	4	4	4	4	4	4	4	4	54

TABLE A.23.6.a Short indentification table for the isolates tested in Wageningen. Greenhouse tests on seedlings, Wageningen, 1959 and 1960. Entries are infection types.

race	isolate	Vilmorin 23-W	Heines Kolben-W	Carstens V-W	Chinese 166-W
W 4	119	0–4	4	0	0
W 6	9789*a*	4^-	0	4	0
	8894	i+4	i–0^+	4^-	i–0
W 8	117	4	0	0	0
	118	4	0^+	0	0
	8097[1])	4^-	0–1	0–1	i
	8125[1])	4	0–1	0–1	i
	8876[1])	4	0	0^+	i
	8881[1])	4	0–1	0–2	0
	9–345*c*	4^-	0	0–1	0
	9–345*d*	4	0^+	i^+	i
	9547	4^-	0	1	0
	9–714*a*	4^-	i–0	i–4	i
W 12	inc.	0	4	0	0
	8147[1])	1–3	4^-	1–2	i
	8700	i–1	4^-	0–4	0
	8861	0	4	0–1	i
	8880	0	4	0–2	0
	8887	0	2–4	$1^{\pm}$	0
	9168	0	4	0	0
	9793	0	4	0	0
W 13	105	0	0	4	4
	113	0^+	0	4	4
	9812	0	0	4	4
W 14	115	0	0	4	0
	116	0	0	4	0
W 16	8130*b*[1])	0–1	0–1	0–2	0
	8153[1])	0–1	0–1	0–1	i
	8589[1])	0	$2^{\pm}$	$2^{\pm}$	i–0
	8600	0	0–1	0	0
	8893	0	0^+	$1^{\pm}$	0^+
	9775	0	0	0	0
	9791*b*	0	$2^{\pm}$	0–2	0
	9792	i	0	0	0
	9798	i	i–0	i–1	0
	9802	0	$2^{\pm}$	0^+	0

[1]) Identification done at 100% RH. Original data corrected to RH = c. 80% level using table 23.32

TABLE A.23.6.b Isolates tested in Wageningen with details on race and origin

+ = unipustular culture	number of isolate	race		sampled variety	provenance	sampling				
		Wageningen key	Braunschweig key			date	GS	TA	DA	F
+	105	W 13	B 27/53	.	Wageningen	.	.	.	.	.
+	113	W 13	B 27/53	.	Wageningen	.	.	.	.	.
+	115	W 14	B $7xV_1$	.	Braunschweig (Germany)	.	.	.	.	.
+	116	W 14	B 17/26	.	Braunschweig (Germany)	.	.	.	.	.
+	117	W 8	B 2x	.	Braunschweig (Germany)	.	.	.	.	.
+	118	W 8	B 55	.	Braunschweig (Germany)		.	.	.	.
+	119	W 4	B 1x	.	Braunschweig (Germany)	.	.	.	.	.
	inc.	W 12	B 54	.	Wageningen	.	.	.	.	.
+	8097	W 8	.	Cappelle	Klinge	20-06-58	10.4	3	2	–
+	8125	W 8	.	Staring	Wolfaartsdijk	21-06-58	10.52	4	4	–
+	8130*b*	W 16	.	Alba	Ramskapelle (Belgium)	18-06-58	10.52	4	7	8
	8147	W 12	.	Flamingo	Kattendijke	21-06-58	10.52	4N	5	–
	8153	W 16	.	Flamingo	Kloetinge	21-06-58	10.52	3N	2	–
+	8589	W 16	.	Heine VII	Houtave (Belgium)	22-04-58	6	4	2	5
+	8600	W 16	.	Heine VII	Hemmen	06-06-58	9	2–3	6	–
+	8700	W 12	.	Heine VII	Almkerk	11-06-58	10.1	4	9	–
	8861	W 12	.	Peko	Philippine	20-06-58	9	4	3	5
	8876	W 8	.	.	Cordoba (Spain)	23-06-58	.	.	.	.
+	8880	W 12	.	Peko	Kattendijke	21-06-58	10.1	4	4	7
+	8881	W 8	.	Staring	Biggekerke	20-06-58	10.52	3	4	5
+	8887	W 12	.	Flamingo	Noordoostpolder	03-07-58	10.52	4	8	–
+	8893	W 16	.	Alba	Wieringerwaard	04-07-58	10.53	4	6	9
	8894	W 14	.	*A. repens*	Noordoostpolder	08-07-58	.	.	.	.
+	8901	W .	.	Peko	Wieringermeer	04-07-58	10.4	4	6	–
	9168	W 12	.	Flamingo	Noordoostpolder	01-04-59	3	4	2	4
+	9–345*c*	W 8	.	Alba	Kattendijke	13-07-59	11.1	2	4	–
+	9–345*d*	W 8		Etoile de Choisy	Kattendijke	13-07-59	11.2	4	8	–
+	9547	W 8	.	Etoile de Choisy	Estrées-St.-Denis (France)	14-06-59	10.54	4	7	8
+	9–714*a*	W 8	.	Cappelle	Montfort l'Amaury (France)	13-06-59	10.52	4	2	6
+	9775	W 16	.	Triumph	Het Bildt	20-07-59	11.2	2N	4E2	–
+	9789*a*	W 6	.	Stella	Vrouwenparochie	05-06-59	10.1	4	6	–
+	9791*b*	W 16	.	Leda	Het Bildt	20-07-59	11.2	–	0E1	–
+	9792	W 16	.	Triumph	Klundert	11-07-59	11.2	2	1	4
+	9793	W 12	.	Flamingo	Kattendijke	21-06-59	11.2	2	5	8
+	9798	W 16	.	Triumph	Noordoostpolder	17-07-59	11.2	4	4E3	–
	9802	W 16	.	Triumph	Het Bildt	20-07-59	11.2	4	9	
	9812	W 13	B 27/53	Reliance	Maran (Switzerland)	25-10-59	10.54	.	+E8	-

Table A.24.31 | Table A.24.32

field number	varieties	Variation in assessment between observers: entries DA local observer	DA writer	[1]	PA local observer	PA writer	entries: date 15–3, GS[2] 3, IL 3	date 15–4, GS[2] 5, IL 7	date 25–4, GS[2] 6, IL 8
1	Carstens V	0	0	.	0	0	0	0	0
2	Chinese 166	0	2	u	0	0	.	.	.
3	Heines 110	0	0	.	0	0	0	0	0
4	Rubis	10	10	.	100	100	0	1	6
5	Vilmorin 27	.	.	.	.	.	.	.	.
6	Probus	.	.	.	.	.	.	.	.
7	Staring	0	0	.	0	0	0	0	0
8	Nord	.	.	.	.	.	.	.	.
9	Cappelle	0	0	.	0	0	0	0	0
10	Triumph	.	.	.	.	.	.	.	.
11	Heines VII	5	7	u	5	25	0	2	3
12	Blé des Dômes	0	3	u	0	0	2	2	3
13	Merlin	.	.	.	.	.	.	.	.
14	Halle 3435/46	.	.	.	.	.	0	0	0
15	Michigan Amber	.	.	.	.	.	2	3	5
16	Medsched × Ridit	.	.	.	.	.	.	.	.
17	Leda	0	2	u	0	0	0	0	3
18	Alba	2	4	u	0	1	.	.	.
19	Bonus	.	.	.	.	.	.	.	.
20	Harvest Queen	10	8	0	100	50	.	.	.
21	Ile de France	0	0	.	0	0	.	.	.
22	Etoile de Choisy	.	.	.	.	.	2	2	3
23	Marne	.	.	.	.	.	.	.	.
24	Carest	.	.	.	.	.	.	.	.
25	Panter	0	0	.	0	0	.	.	.
26	Persian	8	8	.	50	50	0	3	4
27	Reichersberg 42	0	2	u	0	0	0	0	0
28	Heines IV	.	.	.	.	.	.	.	.
29	Flamingo	.	.	.	.	.	.	.	.
30	Stella	.	.	.	.	.	.	.	.
31	Peko	0	2	u	0	0	0	0	1
32	Heines Kolben	4	4	.	1	1	.	.	.
33	Funo	.	.	.	.	.	.	.	.
34	Little Club	.	.	.	.	.	.	.	.
35	Hope × Timstein	.	.	.	.	.	.	.	.
36	Selkirk	0	0	.	0	0	0	0	0
37	Redman	6	5	.	10	5	0	0	3
38	Carpo	.	.	.	.	.	.	.	.
39	Triticum spelta album	0	0	.	0	0	0	0	0
41	Hybrid 46	0	2	u	0	0	0	0	0
42	Frontana	0	0	.	0	0	0	0	3
43	Riebesel 51–52	.	.	.	.	.	.	.	.
45	Mado	.	.	.	.	.	.	.	.
46	Minister	.	.	.	.	.	.	.	.
47	Burgweizen	.	.	.	.	.	.	.	.
48	Jufy I	3	4	.	0	1	0	0	3
49	Prof. Marchal	.	.	.	.	.	.	.	.
50	Falco	.	.	.	.	.	.	.	.
51	Pilote	.	.	.	.	.	3	7	8
52	Opal	.	.	.	.	.	2	3	4

[1]) underestimation u or overestimation o by local observer, as compared to the writer's estimation

[2]) median growth stage of varieties at the date of observation

Variation in successive RIS. a from one trial

DA					RDAP								ARDAP	field number
10–5	23–5	5–6	19–6	1–7	15–3	15–4	25–4	10–5	23–5	5–6	19–6	1–7	1957	
7	8	10.2	10.52	11.1	3	5	6	7	8	10.2	10.52	11.1		
7	9	10	10	10	3	7	8	7	9	10	10	10		
0	0	1	0	3	0	0	0	0	0	0	0	0	0	1
•	•	•	•	•	•	•	•	•	•	•	•	•	•	2
0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
5	9	10	10	10	0	0	37	27	100	100	100	100	100	4
•	•	•	•	•	•	•	•	•	•	•	•	•	•	5
•	•	•	•	•	•	•	•	•	•	•	•	•	•	6
0	0	0	0	2	0	0	0	0	0	0	0	0	0	7
•	•	•	•	•	•	•	•	•	•	•	•	•	•	8
0	0	0	1	1	0	0	0	0	0	0	0	0	0	9
•	•	•	•	•	•	•	•	•	•	•	•	•	•	10
5	7	10	9	9	0	0	1	27	45	100	75	75	87	11
4	6	9	7	4	19	0	1	8	19	75	25	1	50	12
•	•	•	•	•	•	•	•	•	•	•	•	•	•	13
0	0	0	2	0	.	0	0	0	0	0	0	0	0	14
6	7	6	6	3	19	2	12	65	45	10	10	0	10	15
•	•	•	•	•	•	•	•	•	•	•	•	•	•	16
2	1	0	1	0	0	0	1	0	0	0	0	0	0	17
•	•	•	•	•	•	•	•	•	•	•	•	•	•	18
•	•	•	•	•	•	•	•	•	•	•	•	•	•	19
•	•	•	•	•	•	•	•	•	•	•	•	•	•	20
•	•	•	•	•	•	•	•	•	•	•	•	•	•	21
2	2	2	4	4	19	0	1	0	0	0	1	1	0	22
•	•	•	•	•	•	•	•	•	•	•	•	•	•	23
•	•	•	•	•	•	•	•	•	•	•	•	•	•	24
•	•	•	•	•	•	•	•	•	•	•	•	•	•	25
7	8	10	10	9	0	2	5	100	73	100	100	75	100	26
1	0	0	1	0	0	0	0	0	0	0	0	0	0	27
•	•	•	•	•	•	•	•	•	•	•	•	•	•	28
•	•	•	•	•	•	•	•	•	•	•	•	•	•	29
•	•	•	•	•	•	•	•	•	•	•	•	•	•	30
3	5	6	6	2	0	0	0	2	8	10	10	0	10	31
•	•	•	•	•	•	•	•	•	•	•	•	•	•	32
•	•	•	•	•	•	•	•	•	•	•	•	•	•	33
•	•	•	•	•	•	•	•	•	•	•	•	•	•	34
•	•	•	•	•	•	•	•	•	•	•	•	•	•	35
0	0	0	0	2	0	0	0	0	0	0	0	0	0	36
4	7	9	10	9	0	0	1	8	45	75	100	75	87	37
•	•	•	•	•	•	•	•	•	•	•	•	•	•	38
0	0	0	0	0	0	0	0	0	0	0	0	0	0	39
0	0	0	0	0	0	0	0	0	0	0	0	0	0	41
3	6	6	6	7	0	0	1	2	19	10	10	25	10	42
•	•	•	•	•	•	•	•	•	•	•	•	•	•	43
•	•	•	•	•	•	•	•	•	•	•	•	•	•	45
•	•	•	•	•	•	•	•	•	•	•	•	•	•	46
•	•	•	•	•	•	•	•	•	•	•	•	•	•	47
3	6	8	8	8	0	0	1	2	19	50	50	50	50	48
•	•	•	•	•	•	•	•	•	•	•	•	•	•	49
•	•	•	•	•	•	•	•	•	•	•	•	•	•	50
6	7	6	7	1	100	100	100	65	45	10	25	0	17	51
5	7	8	9	3	19	2	5	27	45	50	75	0	62	52

Table A.24.33

field number / varieties	entries: Spontaneous infection: variation between												
	ARDAP												
trial	0001	0004	0005	0007	0008	0010	0013	0014	0017	0020	0021	0022	0025
1 Carstens V	0	8	3	0	0	0	0	0	0	0	0	0	0
2 Chinese 166	0	0	2	0	0	0	0	0	0	0	0	0	0
3 Heines 110	0	0	0	0	0	0	0	0	0	0	0	0	0
4 Rubis	3	0	0	1	0	1	4	0	0	0	0	0	0
5 Vilmorin 27	0	0	0	0	0	0	0	0	0	0	0	0	0
6 Probus	71	19	75	22	34	35	57	47	35	45	39	35	75
7 Staring	0	0	0	0	0	0	0	0	0	0	0	0	0
8 Nord	2	0	0	.	0	0	0	0	0	0	0	0	5
9 Cappelle	0	0	0	0	0	0	0	0	0	0	0	0	5
10 Triumph	71	45	31	35	12	47	71	61	47	59	43	47	62
11 Heines VII	0	0	0	0	0	0	0	1	0	0	0	0	0
12 Blé des Dômes	0	0	0	0	0	0	0	0	0	1	0	0	0
13 Merlin	0	0	0	0	0	0	0	6	0	1	5	0	0
14 Halle 3435/46	0	0	0	0	0	0	0	0	0	0	0	0	0
15 Michigan Amber	.	100	100	47	100	100	100	100	100	100	100	100	100
16 Medsched × Ridit	2	2	0	0	0	3	1	0	3	5	3	3	2
17 Leda	0	0	0	0	0	0	0	0	0	0	0	0	0
18 Alba	0	0	0	0	0	0	0	0	0	0	0	0	0
19 Bonus	0	0	0	0	0	0	0	0	0	0	0	0	0
20 Harvest Queen	55	73	72	100	47	34	71	74	47	73	100	47	87
21 Ile de France	0	0	0	0	.	0	0	0	0	0	0	0	0
22 Etoile de Choisy	0	0	2	0	0	1	0	1	1	0	2	0	0
23 Marne	0	0	0	0	0	0	0	0	0	0	0	0	0
24 Carest	0	0	0	0	0	0	0	0	0	0	0	0	0
25 Panter	0	0	0	0	0	0	0	0	0	0	0	0	0
26 Persian	100	86	87	61	47	74	71	74	61	86	100	86	72
27 Reichersberg 42	0	0	0	0	0	0	0	0	0	0	0	0	0
28 Heines IV	12	8	8	2	9	6	6	22	3	13	2	6	8
29 Flamingo	0	0	0	0	0	0	0	0	0	0	0	0	0
30 Stella	0	0	0	0	0	0	0	0	0	0	0	0	0
31 Peko	0	0	0	0	0	0	0	0	0	0	0	0	0
32 Heines Kolben	0	0	0	0	0	0	0	.	.	0	0	0	0
33 Funo	0	0	0	0	0	0	.	0	.	0	0	0	0
34 Little Club	12	0	10	0	2	5	4	0	0	1	0	0	0
35 Hope × Timstein	.	.	.	.	.	.	.	.	.	.	.	.	.
36 Selkirk	0	0	0	0	0	0	.	.	0	0	0	0	.
37 Redman	57	22	31	34	29	47	56	.	34	73	39	35	59
38 Carpo	0	0	0	0	0	0	0	.	0	0	0	0	0
39 Triticum spelta album	0	0	0	0	0	0	0	0	0	0	0	0	0
41 Hybrid 46	0	0	0	0	0	0	0	0	0	0	0	0	0
42 Frontana	0	0	0	0	0	1	.	0	.	0	0	0	0
43 Riebesel 51–52	0	0	0	0	0	0	0	0	0	0	.	0	0
45 Mado	0	0	0	1	0	0	0	0	0	0	0	0	0
46 Minister	0	0	0	0	0	0	0	0	0	0	0	0	0
47 Burgweizen	0	0	0	0	0	0	0	3	0	0	0	0	0
48 Jufy I	15	0	0	0	0	0	2	1	1	1	6	0	6
49 Prof. Marchal	0	0	0	0	0	0	0	0	0	0	0	0	0
50 Falco	0	0	0	0	0	0	0	1	1	1	0	0	0
51 Pilote	0	0	2	0	0	0	0	0	0	0	0	0	0
52 Opal	0	0	0	0	0	0	0	0	0	0	0	0	0

[1]) underestimation u or overestimation o by local observer, as compared to the writer's estimation
[2]) median growth stage of varieties at the date of observation

trials, subject to identical conditions of infection

0026	0030	0032	0033	0039	0043	0044	0045	0046	0047	0049	0050	0055	0059	0060	number of observations	ARDAP	field number
1	27	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	1
1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	2
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	3
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	4
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	5
9	27	47	47	49	19	25	55	41	22	15	15	9	19	2	2	35	6
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	7
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	8
0	0	0	0	0	0	0	0	0	0	0	0	0	0	.	2	0	9
35	47	47	39	49	45	25	55	71	47	41	57	47	8	19	2	45	10
0	0	0	.	0	0	0	0	0	0	0	0	0	0	0	2	0	11
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	12
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	13
0	0	0	0	0	0	0	0	0	0	0	.	0	0	0	2	0	14
100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	2	98	15
0	1	0	3	0	5	0	15	0	4	1	0	0	0	0	2	2	16
0	0	0	0	0	0	0	6	1	0	0	0	0	0	0	2	0	17
0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	2	0	18
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	19
60	74	47	87	62	86	50	100	.	100	84	71	.	19	45	2	68	20
0	0	0	0	.	0	0	0	0	0	0	0	0	0	0	2	0	21
1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0	22
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	23
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	24
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	25
74	74	74	8	75	59	50	84	86	74	86	72	.	73	19	2	71	26
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	27
6	12	3	0	12	8	3	15	6	6	10	6	1	2	2	2	7	28
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	29
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	30
0	0	0	0	0	0	0	0	0	0	0	.	0	.	.	2	0	31
0	0	1	0	.	.	.	0	0	0	.	.	0	.	.	2	0	32
0	0	0	0	0	0	.	.	0	0	.	.	.	.	.	2	0	33
0	2	0	0	1	0	0	4	0	0	.	.	.	2	0	2	2	34
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	0	35
0	0	0	0	0	.	.	0	0	0	.	.	.	.	.	2	0	36
14	27	27	.	62	.	.	84	42	47	.	.	86	73	.	2	47	37
0	.	0	0	0	0	0	.	0	0	0	.	.	0	.	2	0	38
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	39
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	41
.	0	.	0	0	.	.	0	.	0	.	.	0	0	0	2	0	42
0	0	0	.	0	.	.	.	.	.	.	.	0	0	0	2	0	43
0	0	0	0	0	0	2	1	0	0	0	0	0	0	0	2	0	45
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	46
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	47
1	4	1	2	0	.	.	15	0	1	0	.	.	.	.	2	3	48
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	49
0	1	0	0	0	.	1	3	0	1	0	0	0	0	0	2	0	50
0	0	0	0	0	0	.	.	0	0	.	.	0	0	.	1	0	51
0	0	0	0	0	0	0	0	0	0	0	0	0	0	.	1	0	52

field number	varieties	Table A.24.34 — Spontaneous infection: variations between localities — entries trial: ARDAP 8110	8120	8130	8310	8410	A.24.35 — Spontaneous infection: variations between years — entries year: ARDAP 1958	1959	A.24.37 — Variations between infections artificial and spontaneous — entries infection: ARDAP A	S
1	Carstens V	.	.	.	.	.	.	.	0	1
2	Chinese 166	.	.	.	.	.	0	0	0	0
3	Heines 110	.	.	.	.	.	.	.	0	0
4	Rubis	0	0	0	0	0	100	100	0	0
5	Vilmorin 27	.	.	.	.	.	.	.	2	0
6	Probus	67	65	37	34	8	.	49	85	35
7	Staring	0	0	0	2	0	0	0	5	0
8	Nord	0	2	0	1	0	0	0	1	1
9	Cappelle	0	0	0	1	0	0	0	0	0
10	Triumph	.	.	.	0	0	0	0	67	45
11	Heines VII	0	0	0	0	0	64	47	0	0
12	Blé des Dômes	0	0	0	0	0	20	14	0	0
13	Merlin	.	.	.	0	0	50	100	0	0
14	Halle 3435/46	.	.	.	.	.	.	.	0	0
15	Michigan Amber	92	100	100	100	100	.	87	100	98
16	Medsched × Ridit	.	.	.	.	.	.	.	10	2
17	Leda	0	0	0	0	0	0	0	0	0
18	Alba	0	0	0	0	0	0	0	0	0
19	Bonus	.	.	.	.	.	.	.	0	0
20	Harvest Queen	92	100	100	70	100	79	87	70	68
21	Ile de France	.	.	.	.	.	.	.	1	0
22	Etoile de Choisy	0	0	0	1	0	0	0	1	0
23	Marne	.	.	.	0	0	0	0	0	0
24	Carest	.	.	.	.	.	.	.	0	0
25	Panter	.	.	.	.	.	.	.	0	0
26	Persian	5	27	1	72	8	81	87	70	71
27	Reichersberg 42	.	.	.	.	.	.	.	0	0
28	Heines IV	.	.	.	.	.	17	45	36	7
29	Flamingo	.	.	.	.	.	17	45	1	0
30	Stella	.	.	.	.	.	.	.	0	0
31	Peko	0	0	0	0	0	13	35	0	0
32	Heines Kolben	0	0	0	0	2	.	47	0	0
33	Funo	.	.	.	.	.	.	.	0	0
34	Little Club	0	0	0	0	0	.	61	0	2
35	Hope × Timstein	18	8	5	9	2	.	4	.	.
36	Selkirk	0	0	0	0	.	0	0	0	0
37	Redman	42	2	38	70	8	55	61	67	47
38	Carpo	.	.	.	.	.	.	.	0	0
39	Triticum spelta album	.	.	.	.	.	.	.	0	0
41	Hybrid 46	.	.	.	.	.	.	.	0	0
42	Frontana	.	.	.	.	.	.	.	0	0
43	Riebesel 51–52	.	.	.	.	.	.	.	0	0
45	Mado	.	.	.	.	.	.	.	0	0
46	Minister	.	.	.	.	.	.	.	0	0
47	Burgweizen	.	.	.	.	.	.	.	0	0
48	Jufy I	.	.	.	.	.	.	.	0	3
49	Prof. Marchal	.	.	.	.	.	.	.	0	0
50	Falco	.	.	.	.	.	.	.	0	0
51	Pilote	.	.	.	.	.	.	.	0	0
52	Opal	.	.	.	.	.	.	.	0	0

Table A.23.32 Relation between average infection types and relative humidity RH. For eleven differentials and four races the average infection types are given from three successive readings. The data for the RH = c. 100% are mainly from 1959, those for the RH = c. 80% are from 1960. i types have been excluded from the computations. Entries are average infection type x 10; average number of leaves per entry: 19, range: 3 – 50.

differential varieties	RH (av.)	W 8			W 12			W 13			W 16			race
		1st	2nd	3rd	1st	2nd	3rd	1st	2nd	3rd	1st	2nd	3rd	reading
	100	14	17	20	14	16	18	13	16	.	15	17	19	average day of reading
	80	15	17	19	17	19	22	14	16	18	17	19	22	
1 Michigan Amber	100	37	40	.	40	40	40	37	40	.	36	39	39	
	80	40	40	40	40	40	40	40	40	40	34	34	34	
2 Blé rouge d'Écosse	100	21	27	.	40	40	40	40	40	.	31	40	40	
	80	11	13	16	24	22	27	33	33	27	34	32	34	
3 Strubes Dickkopf	100	29	40	.	40	36	.	40	40	.	33	40	40	
	80	25	28	32	17	32	35	15	19	18	3	18	22	
4 Webster	100	11	16	.	12	13	16	9	11	.	7	10	11	
	80	20	21	21	6	13	15	18	20	22	5	12	14	
5 Holzapfels Frühweizen	100	26	29	.	30	32	.	39	40	.	18	26	25	
	80	9	15	14	12	24	26	25	29	29	7	10	11	
6 Vilmorin 23	100	28	28	.	3	9	9	9	19	.	7	9	8	
	80	26	33	34	0	0	0	2	2	2	0	0	0	
7 Heines Kolben	100	2	5	.	39	40	40	0	0	.	5	11	14	
	80	4	5	4	26	36	40	5	5	5	5	7	7	
8 Carstens V	100	24	28	.	10	21	30	40	40	.	3	11	10	
	80	0	0	2	0	2	4	34	34	35	1	2	3	
9 Spaldings prolific	100	3	10	17	12	23	6	2	14	.	5	4	12	
	80	0	0	0	0	6	10	3	7	18	3	13	17	
10 Chinese 166	100	33[1]	33[1]	.	23[1]	20[1]	.	33	30	.	4	9	9	
	80	0	0	0	.	.	.	29	33	33	0	0	0	
11 Rouge prolif. barbu	100	10	19	.	3	19	7	4	18	.	3	16	24	
	80	0	0	1	0	2	3	5	5	3	0	0	0	

[1]) high value due to combination of great number of i types (excluded from computation) with high percentage of impurities, giving type 4 reactions

TABLE A.24.42 Race and population characteristics according to field tests. Entries are ARDAP.s or, in the case of RC.s and PC.s, $\overline{\text{ARDAP}}$.s. An abstract of this table is given in table 24.42.

TABLE A.24.42.	a	b			c				d			
race/population	$7xV_1$	Heines VII			Leda isolates				Heines VII-Heines IV			
infection	A	A	A		A	A	A		A	A	A	
year	60	60	60		60	60	60		56	56	56	
trial	0019	0052	0038		0012	0035	0056		2210	2240	2253	
field number isolate RC/PC	115	8589	8600	RC	9791*a*	9791*b*	9791*b*	RC	B7x	B7x	B7x	RC
1 Carstens V	0	0	0	0	0	0	0	0	0	0	0	0
2 Chinese 166	2	0	4	2	0	0	0	0	.	.	.	.
3 Heines 110	0	0	0	0	0	0	0	0	0	0	0	0
4 Rubis	73	82	100	93	86	52	100	77	.	.	.	.
5 Vilmorin 27	0	0	0	0	0	0	0	0	–	–	0	0
6 Probus	–	–	54	54	–	–	–	–	.	.	.	.
7 Staring	0	0	0	0	0	0	0	0	–	–	1	1
8 Nord	0	0	0	0	0	0	0	0	–	–	1	1
9 Cappelle	0	0	0	0	0	0	0	0	–	–	0	0
10 Triumph	–	–	2	2	–	–	–	–	.	.	.	.
11 Heines VII	0	36	44	41	64	11	12	38	79	100	75	82
12 Blé des Dômes	0	5	2	3	15	2	5	9	53	.	100	65
13 Merlin	0	36	27	31	46	6	5	26	.	.	.	.
14 Halle 3435/46	0	0	0	0	0	0	.	0	.	.	.	.
15 Michigan Amber	–	–	62	62	–	–	–	–	–	–	.	.
16 Medsched × Ridit	0	–	13	13	–	–	–	–	.	.	.	.
17 Leda	0	0	0	0	40	2	0	21	.	.	.	.
18 Alba	0	0	1	1	14	2	0	8	.	.	.	.
19 Bonus	0	0	0	0	0	0	0	0	.	.	.	.
20 Harvest Queen	–	–	52	52	–	–	–	–	.	.	.	.
21 Ile de France	0	0	0	0	4	0	0	2	–	–	0	0
22 Etoile de Choisy	0	0	0	0	4	0	1	2	0	0	0	0
23 Marne	0	0	0	0	0	0	0	0	0	0	0	0
24 Carest	0	0	0	0	0	0	0	0	.	.	.	.
25 Panter	0	0	0	0	0	0	0	0	0	1	1	0
26 Persian	–	–	33	33	–	–	–	–	.	.	.	.
27 Reichersberg 42	0	0	0	0	0	2	0	0	0	0	0	0
28 Heines IV	–	–	2	2	29	5	12	18	26	50	75	41
29 Flamingo	1	0	1	1	15	2	12	10	.	.	.	.
30 Stella	0	0	0	0	3	2	5	3	.	.	.	.
31 Peko	0	0	0	0	4	0	5	3	1	0	0	1
32 Heines Kolben	0	0	.	0	4	0	12	4	.	.	.	.
33 Funo	0	.	.	.	0	0	0	0	–	–	0	0
34 Little Club	22	86	33	54	63	100	5	66	.	.	.	.
35 Hope × Timstein	.	.	.	.	.	.	.	.	.	.	.	.
36 Selkirk	0	.	.	.	.	0	0	0	.	.	0	0
37 Redman	–	–	.	.	–	–	–	–	.	.	.	.
38 Carpo	0	0	0	0	0	0	0	0	.	.	.	.
39 Triticum spelta album	0	0	0	0	0	0	0	0	.	.	.	.
41 Hybrid 46	0	0	0	0	0	0	0	0	0	0	0	0
42 Frontana	.	0	.	0	2	0	5	2	.	.	.	.
43 Riebesel 51-52	0	.	0	0	0	0	.	0	.	.	.	.
45 Mado	0	0	0	0	1	2	0	1	.	.	.	.
46 Minister	0	0	0	0	0	0	0	0	0	0	0	0
47 Burgweizen	0	0	0	0	0	0	0	0	.	.	.	.
48 Jufy I	0	1	18	11	–	–	–	–	–	–	75	75
49 Prof. Marchal	0	5	13	10	14	2	5	8	.	.	.	.
50 Falco	0	–	0	0	4	2	.	3	.	.	.	.
51 Pilote	0	0	0	0	0	0	0	0	.	.	.	.
52 Opal	0	0	.	0	0	0	0	0	.	.	.	.
weight	1.1.2	2	3	1.2.5	3	2	1	1.3.6	3	1	1	1.3.5

. = no data available
– = data rejected because of possible spontaneous infection

e								f						
Flamingo								Peko						
A	A	A	A	S	S	S		A	A	A	A	A		
60	60	60		58	59			58	59	59	60	60		
0034	0037	0048		3520	3520			3671	3675	3674	0028	0053		
9168	9793	8887		.	.		RC	6900	8700	8901	8700	8880	RC	
0	0	0	0	0	.	0	0	2	0	0	0	0	0	1
0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
0	0	0	0	0	1	0	0	0	0	0	0	0	0	3
72	88	100	87	100	100	100	94	84	100	100	85	84	90	4
0	0	0	0	.	0	0	0	18	0	0	0	0	3	5
–	–	–	–	.	35	35	35	9	48	9	46	18	28	6
0	0	0	0	0	0	0	0	0	0	0	0	0	0	7
0	0	0	0	0	0	0	0	.	0	0	0	0	0	8
0	0	0	0	0	0	0	0	0	0	0	0	0	0	9
–	–	–	–	0	0	0	0	0	0	0	0	0	0	10
18	30	31	27	53	37	48	39	72	74	35	58	7	50	11
3	4	7	5	17	11	15	11	0	6	1	5	1	3	12
8	15	31	18	50	100	67	46	86	.	.	27	18	41	13
0	0	.	0	.	1	1	1	0	0	0	0	0	0	14
–	–	–	–	.	92	92	92	100	100	88	85	100	94	15
–	–	–	–	.	4	4	4	19	.	.	37	0	21	16
0	0	0	0	0	0	0	0	0	0	0	0	0	0	17
0	0	2	0	0	0	0	0	0	0	0	5	0	1	18
0	0	0	0	.	0	0	0	0	0	0	0	0	0	19
–	–	–	–	66	92	75	75	86	74	62	100	56	76	20
0	0	0	0	0	0	0	0	0	0	0	0	0	0	21
0	0	0	0	0	0	0	0	0	0	0	2	0	0	22
6	0	0	2	0	0	0	1	.	0	0	0	0	0	23
0	0	0	0	.	.	.	0	.	.	.	0	0	0	24
0	0	0	0	0	.	0	0	0	0	0	0	0	0	25
–	–	–	–	67	92	75	75	84	74	62	67	72	71	26
.	0	0	0	0	.	0	0	0	0	.	0	0	0	27
–	–	–	–	17	78	37	37	.	0	0	0	0	0	28
11	4	8	7	17	78	37	24	0	0	0	6	0	2	29
0	0	5	1	.	.	.	1	0	0	.	1	0	0	30
3	2	5	4	11	23	15	10	69	73	35	8	12	37	31
56	.	23	39	.	64	64	53	.	88	.	39	18	47	32
0	.	0	0	.	0	0	0	0	0	0	0	0	0	33
56	.	43	49	.	73	73	63	.	88	62	67	56	68	34
.	.	.	.	.	3	3	3	.	0	0	.	.	0	35
0	.	0	0	0	.	0	0	.	0	0	0	0	0	36
–	.	.	.	46	73	55	55	.	88	49	8	31	40	37
0	.	0	0	.	.	.	0	0	.	.	0	0	0	38
0	0	0	0	0	0	0	0	0	0	0	0	0	0	39
0	0	0	0	0	.	0	0	0	0	0	0	0	0	41
.	0	0	0	4	.	4	2	.	0	.	6	0	3	42
0	0	.	0	.	.	.	0	.	0	0	.	.	0	43
0	0	0	0	.	.	.	0	0	0	0	0	0	0	45
0	0	0	0	.	.	.	0	0	0	0	0	0	0	46
0	1	0	0	.	.	.	0	.	0	0	6	0	2	47
–	–	–	–	25	.	25	25	0	0	.	11	0	4	48
0	4	7	4	.	.	.	4	.	0	.	5	0	2	49
0	0	.	0	.	.	.	0	0	.	.	0	0	0	50
0	0	0	0	.	.	.	0	.	.	.	0	.	0	51
0	0	0	0	.	.	.	0	0	.	.	0	0	0	52
2	3	2	1.3.7	6	3	2.2.9	3.5.16	2	2	2	3	2	3.5.11	
								Peko Baarn sand	H VII Baarn sand	Peko Baarn sand	H VII OFL clay	Peko OFL clay	[1]	

[1]) see text (24.42)

Table A.24.42.

field number	Table A.24.42 race/population	g Heines Kolben					h Chinese				
	infection	A	A	A	A		A	A	A	A	
	year	60	60	60	60		59	60	60	60	
	trial	3679*a*	3679*b*	3689	0009		2252	367	0031	0054	
	isolate RC/PC	119	119	119	119	RC	B27/53	105	113	113	RC
1	Carstens V	0	0	0	0	0	0	16	37	12	16
2	Chinese 166	0	.	.	1	0	75	100	100	84	92
3	Heines 110	.	0	0	0	0	0	0	0	0	0
4	Rubis	100	100	100	100	100	0	0	0	8	2
5	Vilmorin 27	0	0	1	0	0	0	0	0	0	0
6	Probus	3	3	13	–	6	27	30	68	69	45
7	Staring	0	0	3	0	0	0	0	0	0	0
8	Nord	1	0	2	0	1	0	0	0	0	0
9	Cappelle	.	0	0	0	0	0	0	0	0	0
10	Triumph	0	0	0	–	0	0	1	1	1	1
11	Heines VII	0	0	1	0	0	0	0	0	0	0
12	Blé des Dômes	3	0	3	4	2	0	0	0	0	0
13	Merlin	0	0	0	0	0	0	0	0	0	0
14	Halle 3435/46	0	0	0	1	0	0	0	0	0	0
15	Michigan Amber	100	100	100	–	100	100	87	100	100	95
16	Medsched × Ridit	0	0	2	0	0	0	0	1	3	1
17	Leda	0	0	0	0	0	0	0	0	0	0
18	Alba	9	1	0	1	3	0	0	0	0	0
19	Bonus	0	1	1	0	1	0	0	0	0	0
20	Harvest Queen	91	72	59	–	74	87	87	84	100	89
21	Ile de France	0	0	0	1	0	0	0	0	0	0
22	Etoile de Choisy	0	0	0	0	0	0	.	0	2	1
23	Marne	0	0	0	0	0	0	0	0	0	0
24	Carest	0	0	0	0	0	.	0	0	0	0
25	Panter	0	0	0	0	0	0	0	0	0	0
26	Persian	53	55	19	–	42	27	46	84	48	50
27	Reichersberg 42	0	0	0	0	0	0	0	0	0	0
28	Heines IV	0	0	0	–	0	0	0	0	0	0
29	Flamingo	0	2	0	0	0	0	0	0	0	0
30	Stella	3	0	0	0	1	.	0	0	0	0
31	Peko	12	.	.	2	8	.	0	.	0	0
32	Heines Kolben	91	82	88	32	77	.	0	0	0	0
33	Funo	1	0	0	0	0	1	2	0	0	1
34	Little Club	100	90	69	46	79	.	0	0	6	1
35	Hope × Timstein	.	.	.	.	.	.	.	.	.	.
36	Selkirk	0	.	1	0	0	.	4	0	0	2
37	Redman	73	27	38	–	46	.	78	18	2	35
38	Carpo	0	0	0	0	0	.	0	0	0	0
39	Triticum spelta album	0	.	.	0	0	0	0	0	0	0
41	Hybrid 46	0	0	6	0	0	0	0	0	0	0
42	Frontana	2	.	.	0	1	.	0	0	.	0
43	Riebesel 51-52	0	0	0	0	0	.	0	0	.	0
45	Mado	2	0	1	0	1	0	1	0	0	0
46	Minister	0	8	3	0	3	0	0	0	0	0
47	Burgweizen	0	0	0	0	0	.	4	0	0	0
48	Jufy I	21	0	0	–	10	.	17	2	0	9
49	Prof. Marchal	3	0	1	0	1	.	3	0	0	1
50	Falco	3	0	5	4	3	.	2	0	0	1
51	Pilote	0	0	0	0	0	.	0	0	.	0
52	Opal	.	0	0	0	0	.	.	0	.	0
	weight	3	3	3	2	1.4.11	2	4	2	2	2.4.10

. = no data available

– = data rejected because of possible spontaneous infection

i								j					
Cappelle								Triumph					
A	A		A		A	S		A	A	A	S		
56	56		56		56	57		60	60		60		
2210	2240		2253		.	2470		0018	0003		[3]		
B2x+B7x	B2x+B7x	[1]	B7x	[2]	2	.	RC	9775	9798	ARDAP	0018	RC	
0	0	0	0	0	0	.	0	0	0	0	1	1	1
.	.	.	.	.	0	.	0	0	0	0	0	0	2
0	0	0	0	0	.	.	0	0	0	0	0	0	3
.	.	.	.	.	.	.	.	0	0	0	0	0	4
6	10	7	0	7	.	.	7	2	1	1	0	0	5
.	.	.	.	.	.	.	.	71	86	78	35	38	6
8	10	8	1	8	47	29	24	2	4	3	0	0	7
63	75	66	1	66	.	.	66	0	1	0	0	0	8
6	50	14	0	14	34	20	20	0	0	0	0	0	9
.	.	.	.	.	.	.	.	72	69	70	45	47	10
79	100	84	75	–	0	–	0	0	0	0	0	0	11
53	.	53	100	–	.	.	–	0	0	0	0	0	12
.	.	.	.	.	.	.	.	0	0	0	0	0	13
.	.	.	.	.	.	.	.	0	0	0	0	0	14
57	100	68	1	68	100	–	100	100	100	100	98	98	15
.	.	.	.	.	.	.	.	18	1	9	2	2	16
.	.	.	.	.	0	.	0	0	1	0	0	0	17
.	.	.	.	.	.	.	.	0	0	0	0	0	18
.	.	.	.	.	.	.	.	0	0	0	0	0	19
.	.	.	.	.	.	.	.	41	72	36	68	67	20
5	50	16	0	16	.	.	16	0	1	0	0	0	21
0	0	0	0	0	.	.	0	2	1	1	0	0	22
0	0	0	0	0	.	.	0	0	0	0	0	0	23
.	.	.	.	.	.	.	.	0	0	0	0	0	24
0	1	0	1	0	0	.	0	0	0	0	0	0	25
.	.	.	.	.	.	–	–	41	100	70	71	71	26
0	0	0	0	0	0	.	0	0	0	0	0	0	27
26	50	32	75	–	.	.	–	6	55	30	7	9	28
.	.	.	.	.	.	.	.	2	0	1	0	0	29
.	.	.	.	.	.	.	.	0	0	0	0	0	30
1	0	1	0	1	0	.	1	0	0	0	0	0	31
.	.	.	.	.	0	.	0	0	0	0	0	0	32
4	1	3	0	3	.	.	3	0	0	0	0	0	33
.	.	.	.	.	.	.	.	0	0	0	2	2	34
.	.	.	.	.	.	.	.	.	.	.	0	0	35
.	.	.	0	.	.	.	0	.	0	0	0	0	36
.	.	.	.	.	.	–	.	15	86	50	47	47	37
.	.	.	.	.	.	.	.	0	0	0	0	0	38
.	.	.	.	.	.	.	.	0	0	0	0	0	39
0	0	0	0	0	.	.	0	0	0	0	0	0	41
.	.	.	.	.	.	.	.	.	0	0	0	0	42
.	.	.	.	.	.	.	.	.	0	0	0	0	43
.	.	.	.	.	.	.	.	0	0	0	0	0	45
0	0	0	0	0	.	.	0	0	0	0	0	0	46
.	.	.	.	.	.	.	.	0	0	0	0	0	47
82	100	86	75	–	.	–	–	0	13	6	3	3	48
.	.	.	.	.	.	.	.	0	0	0	0	0	49
.	.	.	.	.	.	.	.	0	4	2	0	0	50
.	.	.	.	.	.	.	.	0	0	0	0	0	51
.	.	.	.	.	.	.	.	0	0	0	0	0	52
3	1	1.2.4	1	1.2.4	2	3	2.4.9	2	2	1.2.4	1.28.54	1.30.58	

[1] ARDAP of combined infection by races B2x and B7x

[2] ARDAP of race B2x after subtraction of all data, supposed to be due to race B7x

[3] from table A.24.33

TABLE A.24.42

field number — Table A.24.42.	k				l				m
race/population	Alba				Etoile de Choisy				Heines IV
infection	A	A	A		A	A	A		A
year	58	59	60		60	60	60		59
trial	3672	3672	0029		0024	0051	0041		2250
isolate RC/PC	8130*b*	8130*b*	8893	RC	9–345*d*	9–345*d*	9547	RC	B7x
1 Carstens V	0	0	0	0	2	0	0	1	0
2 Chinese 166	0	1	0	0	0	0	0	0	.
3 Heines 110	0	0	0	0	0	0	0	0	0
4 Rubis	0	0	0	0	0	5	0	1	4
5 Vilmorin 27	0	0	0	0	0	0	0	0	0
6 Probus	.	46	40	43	–	–	–	–	56
7 Staring	0	0	0	0	3	0	0	1	0
8 Nord	.	1	0	0	27	1	6	14	0
9 Cappelle	0	0	0	0	0	0	1	0	0
10 Triumph	0	0	1	0	–	–	–	–	0
11 Heines VII	0	0	0	0	0	0	0	0	0
12 Blé des Dômes	0	0	0	0	0	1	0	0	0
13 Merlin	2	.	0	0	0	0	0	0	0
14 Halle 3435/46	.	0	0	0	0	0	0	0	8
15 Michigan Amber	.	100	100	100	–	–	–	–	90
16 Medsched × Ridit	.	1	0	0	–	–	–	–	12
17 Leda	0	0	1	0	0	0	0	0	0
18 Alba	42	87	8	46	0	1	0	0	0
19 Bonus	0	0	0	0	0	0	0	0	0
20 Harvest Queen	.	100	40	70	–	–	–	–	72
21 Ile de France	.	0	0	0	0	0	0	0	0
22 Etoile de Choisy	0	0	0	0	6	5	3	5	0
23 Marne	.	0	0	0	8	5	3	6	.
24 Carest	.	.	0	0	11	5	1	6	.
25 Panter	0	0	0	0	0	0	0	0	.
26 Persian	.	73	19	46	–	–	–	–	83
27 Reichersberg 42	0	.	0	0	0	0	0	0	.
28 Heines IV	.	0	0	0	–	–	–	–	75
29 Flamingo	0	0	0	0	0	0	0	0	0
30 Stella	0	0	0	0	0	0	0	0	.
31 Peko	0	0	0	0	0	0	0	0	.
32 Heines Kolben	.	0	0	0	0	0	.	0	.
33 Funo	.	0	0	0	0	0	.	0	.
34 Little Club	.	1	0	0	0	0	0	0	.
35 Hope × Timstein	.	0	.	0	.	.	.	.	.
36 Selkirk	.	0	0	0	0	.	0	0	.
37 Redman	.	45	18	31	–	–	–	–	.
38 Carpo	0	.	0	0	0	0	0	0	.
39 Triticum spelta album	0	0	0	0	0	0	0	0	0
41 Hybrid 46	.	0	0	0	0	0	0	0	.
42 Frontana	.	0	.	0	0	0	.	0	.
43 Riebesel 51-52	0	.	0	0	0	.	.	0	.
45 Mado	0	0	3	1	0	5	0	1	.
46 Minister	0	0	0	0	0	0	0	0	.
47 Burgweizen	.	0	0	0	0	5	0	1	0
48 Jufy I	.	0	8	4	–	–	–	–	.
49 Prof. Marchal	.	0	0	0	0	0	0	0	.
50 Falco	.	.	3	3	1	5	1	2	.
51 Pilote	.	.	0	0	0	0	.	0	.
52 Opal	.	.	0	0	0	0	.	0	.
weight	1	2	2	3.3.5	3	2	2	1.3.7	1.1.3

. = no data available

– = data rejected because of possible spontaneous infection

n Probus																
S 56 8310 .	S 57 8310 .	S 58 8540 .	S 59 8110 .	S 59 8120 .	S 59 8130 .	S 59 8310 .	S 59 8410 .	S 60 8110 .	S 60 8120 .	S 60 8130 .	S 60 8210 .	S 60 8310 .	S 60 8410 .	S 60 853 .	PC/RC	
.	0	.	.	.	.	.	.	0	0	0	0	0	0	.	0	1
.	.	0	.	.	.	.	.	0	0	0	0	0	0	.	0	2
.	.	.	0	0	0	0	0	0	0	0	0	0	0	.	0	3
.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4
.	.	.	2	0	0	1	0	0	2	0	0	0	0	.	0	5
.	.	.	67	65	36	38	8	62	18	75	0	19	2	75	42	6
.	5	7	0	0	0	2	0	0	0	0	0	0	0	0	1	7
.	.	.	0	2	0	1	0	0	0	0	0	0	0	0	0	8
.	0	0	0	0	0	1	0	0	0	0	0	5	0	1	0	9
.	.	.	.	.	.	.	.	0	0	0	0	0	0	1	0	10
.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11
.	0	0	0	0	0	0	0	0	0	0	0	0	0	.	0	12
.	.	.	.	.	.	.	.	0	0	0	0	0	0	.	0	13
.	.	.	0	0	0	0	0	0	0	0	0	0	0	.	0	14
.	.	.	92	100	100	100	100	100	100	100	100	100	100	100	99	15
.	.	.	0	0	0	0	0	0	0	0	0	0	0	.	0	16
.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	17
.	.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	18
.	.	.	0	0	0	0	0	0	0	0	0	0	0	.	0	19
.	100	100	92	100	100	69	100	62	63	100	17	100	42	100	81	20
.	.	.	0	0	0	0	0	0	0	0	0	0	0	.	0	21
.	19	.	0	0	0	0	0	0	0	0	0	0	0	1	1	22
.	.	.	.	.	.	.	.	0	0	0	0	0	0	1	0	23
.	.	.	.	.	.	.	.	0	0	0	0	0	0	.	0	24
.	0	.	.	.	.	.	.	0	0	0	0	0	0	.	0	25
.	19	17	5	27	1	72	8	15	21	75	1	0	17	75	26	26
.	0	.	.	.	.	.	.	0	0	0	0	0	0	.	0	27
.	.	.	.	.	.	.	.	0	0	0	0	0	0	.	0	28
.	.	.	.	.	.	.	.	0	0	0	0	0	0	0	0	29
.	.	.	.	.	.	.	.	0	0	0	0	0	0	.	0	30
0	0	.	0	0	0	0	0	0	0	0	.	0	0	.	0	31
.	.	.	0	0	0	0	2	0	0	0	.	0	0	.	0	32
0	0	.	0	0	0	0	.	0	0	0	.	0	0	.	0	33
.	.	.	0	0	0	0	.	0	0	0	.	0	0	.	0	34
.	.	.	18	8	5	6	0	15	44	50	.	0	0	.	15	35
0	0	.	0	0	0	0	.	0	0	0	.	0	0	.	0	36
100	19	.	42	2	36	69	8	7	21	75	.	.	17	.	37	37
.	.	.	.	.	.	.	.	0	0	0	.	0	0	.	0	38
.	0	0	0	0	0	0	0	0	0	0	.	0	0	0	0	39
.	0	.	.	.	.	.	.	.	.	.	.	.	.	.	0	41
.	0	.	.	.	.	.	.	.	.	.	.	.	.	.	0	42
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	43
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	45
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	46
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	47
.	19	.	.	.	.	.	.	.	.	.	.	.	.	.	19	48
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	49
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	50
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	51
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	52
1	1	1	3	1	2	3	1	2	2	1	1	1	1	1	5.15.22	

field number	TABLE A.24.42.	o					p	q			
	race/population	2x/55					7x	Grecian			
	infection	A	A	A	A		A	S	S	S	
	year	60	60	60	60		60	60	60	60	
	trial	2254	3677	3678	3688		2250	9610	9620	9630	
	isolate RC/PC	B55	117	118	118	RC	B7x	.	.	.	PC
1	Carstens V	1	0	0	0	0	0	.	.	.	.
2	Chinese 166	0	1	0	.	0	0	.	.	.	.
3	Heines 110	0	0	0	0	0	0	.	.	.	.
4	Rubis	1	0	0	0	0	0	84	17	53	58
5	Vilmorin 27	2	2	0	2	2	0	.	.	.	.
6	Probus	6	11	2	8	7	52	2	2	0	1
7	Staring	0	1	0	0	0	0	0	2	4	2
8	Nord	4	6	0	4	3	0	0	2	1	1
9	Cappelle	2	4	0	0	2	1	0	2	4	2
10	Triumph	0	0	0	0	0	12	2	2	1	2
11	Heines VII	0	0	0	0	0	0	0	0	1	0
12	Blé des Dômes	0	0	0	0	0	0	.	.	.	.
13	Merlin	0	0	0	0	0	0	.	.	.	.
14	Halle 3435/46	1	0	0	0	0	1	.	.	.	.
15	Michigan Amber	100	100	100	100	100	100	100	100	100	100
16	Medsched × Ridit	0	0	0	0	0	1	.	.	.	.
17	Leda	0	0	0	.	0	0	0	2	2	1
18	Alba	5	7	8	22	10	0	0	2	4	2
19	Bonus	0	0	0	0	0	0	.	.	.	.
20	Harvest Queen	73	61	87	81	75	51	31	100	58	56
21	Ile de France	0	0	0	0	0	0	.	.	.	.
22	Etoile de Choisy	2	0	0	0	0	0	6	2	1	3
23	Marne	0	0	0	0	0	0	0	2	1	1
24	Carest	1	0	0	2	1	0	.	.	.	.
25	Panter	0	0	0	0	0	0	.	.	.	.
26	Persian	83	20	62	20	45	36	69	70	9	45
27	Reichersberg 42	0	0	0	0	0	0	.	.	.	.
28	Heines IV	0	0	0	0	0	2	.	.	.	.
29	Flamingo	0	0	0	0	0	0	0	2	0	0
30	Stella	0	0	0	0	0	0	.	.	.	.
31	Peko	0	0	0	.	0	0	.	.	.	.
32	Heines Kolben	0	0	0	0	0	0	.	.	.	.
33	Funo	0	0	0	0	0	0	.	.	.	.
34	Little Club	0	.	0	0	0	0	.	.	.	.
35	Hope × Timstein	0	0	0	.	0	0	.	.	.	.
36	Selkirk	0	0	0	.	0	0	.	.	.	.
37	Redman	4	46	67	73	49	2	.	.	.	.
38	Carpo	0	0	0	0	0	0	.	.	.	.
39	Triticum spelta album	0	0	0	.	0	0	0	2	1	1
41	Hybrid 46	.	0	0	2	0	.	.	.	.	.
42	Frontana	.	2	0	.	1	.	.	.	.	.
43	Riebesel 51-52	.	0	0	0	0	.	.	.	.	.
45	Mado	.	0	0	2	1	.	.	.	.	.
46	Minister	.	0	0	0	0	.	.	.	.	.
47	Burgweizen	.	0	0	0	0	.	.	.	.	.
48	Jufy I	.	3	25	25	17	.	.	.	.	.
49	Prof. Marchal	.	0	0	0	0	.	.	.	.	.
50	Falco	.	3	5	33	12	.	.	.	.	.
51	Pilote	.	0	0	.	0	.	.	.	.	.
52	Opal	.	0	0	0	0	.	.	.	.	.
	weight	3	4	4	3	1.4.14	1.1.3	2	1	2	1.3.5

. = no data available

– = data rejected because of possible spontaneous infection

r							s					t				
Iberian							Levantine					Kenya				
S	S	S	S	S	S		S	S	S	S		S	S	S		
58	58	59	59	59	60		59	60	60	60		59	60	60		
9730	9750	9510	9520	9750	9510		9011	9011	9910	9420		9031	9031	9032		
.	.	.	.	.	.	PC	.	.	.	.	PC	.	.	.	PC	
.	.	.	.	.	0	0	.	.	.	0	0	.	.	.	.	1
0	0	.	.	.	0	0	.	.	.	0	0	.	.	.	.	2
.	.	0	0	0	0	0	.	.	.	0	0	.	.	.	.	3
100	100	5	100	25	100	65	.	.	.	1	1	.	.	.	.	4
.	.	0	0	0	0	0	.	.	.	0	0	.	.	.	.	5
.	.	5	27	2	42	12	.	.	.	0	0	.	.	.	.	6
0	24	0	8	0	42	10	.	.	.	0	0	.	.	.	.	7
.	.	10	27	0	70	17	.	.	.	0	0	.	.	.	.	8
1	5	0	27	0	42	7	.	.	.	0	0	.	.	.	.	9
.	.	.	.	.	7	7	.	.	.	0	0	.	.	.	.	10
0	0	0	0	0	100	8	.	.	.	0	0	.	.	.	.	11
0	18	0	27	0	0	7	.	.	.	0	0	.	.	.	.	12
.	.	.	.	.	17	17	.	.	.	0	0	.	.	.	.	13
.	.	0	0	0	0	0	.	.	.	0	0	.	.	.	.	14
.	.	100	100	100	100	100	.	.	.	100	100	.	.	.	.	15
.	.	0	0	0	0	0	.	.	.	0	0	.	.	.	.	16
0	0	0	0	0	7	0	.	.	.	0	0	.	.	.	.	17
0	0	5	8	0	0	1	.	.	.	0	0	.	.	.	.	18
.	.	0	0	0	0	0	.	.	.	0	0	.	.	.	.	19
2	91	3	100	29	70	45	.	.	.	1	1	.	.	.	.	20
.	.	0	0	0	0	0	.	.	.	0	0	.	.	.	.	21
.	.	0	0	0	42	6	.	.	.	0	0	.	.	.	.	22
.	.	.	.	.	0	0	.	.	.	0	0	.	.	.	.	23
.	.	.	.	.	0	0	.	.	.	0	0	.	.	.	.	24
.	.	.	.	.	0	0	.	.	.	0	0	.	.	.	.	25
17	86	2	100	42	17	45	.	.	.	5	5	.	.	.	.	26
.	.	.	.	.	0	0	.	.	.	0	0	.	.	.	.	27
.	.	.	.	.	0	0	.	.	.	0	0	.	.	.	.	28
.	.	.	.	.	0	0	.	.	.	0	0	.	.	.	.	29
.	.	.	.	.	0	0	.	.	.	0	0	.	.	.	.	30
.	.	0	0	0	0	0	0	100	0	.	33	33	3	0	17	31
.	.	0	0	0	0	0	0	57	0	.	19	35	6	0	19	32
.	.	0	0	0	.	0	0	.	0	.	0	12	2	0	6	33
.	.	5	100	20	42	18	100	57	100	.	86	100	100	100	100	34
.	.	0	0	0	0	0	0	57	+	.	28	87	8	37	55	35
.	.	0	0	0	0	0	57	57	+	.	57	87	100	75	87	36
.	.	7	8	12	.	10	57	57	50	.	55	80	58	62	70	37
.	.	.	.	.	0	0	.	0	0	.	0	.	0	0	0	38
0	0	0	0	0	0	0	0	57	0	.	19	0	0	0	0	39
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	41
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	42
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	43
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	45
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	46
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	47
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	48
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	49
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	50
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	51
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	52
2	3	2	1	3	1	3.6.12	1	1	1	1	2.4.4	4	2	2	2.3.8	

TABLE A.24.51 Review of European yellow rust epidemics

Year	Country	Region	Crop	Remarks	Author
1794	Sweden	Westergötland	rye	severe	BJERKANDER. ex E. & H. [1]
1804	England	–	–	severe	BANKS, ex E. & H.
1846	Germany	Baden (Freiburg)	rye	severe, on heads	BRAUN, 1846
	Germany	Rheinland	rye	severe, great losses	TREVIRANUS, 1846
1863	Denmark	–	wheat	great losses	ÖRSTED, ex E. & H.
1874	Denmark	–	wheat and rye	important autumn infection	NIELSEN, ex E. & H.
1882	England	Norfolk, Suffolk	–	–	PLOWRIGHT. ex E. & H.
1889	Sweden	–	wheat	mild	E. & H.
1890	Sweden	Östergötland, Malmö	wheat, especially "Dutch" wheats	very severe, great losses	E. & H.
1892	Sweden	–	wheat	severe	E. & H.
1903	Germany	Württemberg	wheat	severe	HILTNER, 1905
1904	Germany	Bayern	wheat	severe, mainly local farmers varieties	HILTNER, 1905
1907	Germany	Posen, W-Preussen	wheat, var. Extra Squarehead	heavily infected	KIRCHNER, 1916
1913	Austria	Wien	wheat	important autumn infection	HECKE, 1915
	France	Lyon	barley	also on heads	BLARINGHEM, 1914
1914	Austria	Wien	wheat	general, considerable damage	HECKE, 1915
	Germany	Bayern	rye, Petkus; wheat, squareheads	mainly on rye	HILTNER, 1914
	Germany	Halle/Saale	wheat	losses 20 %.	MÜLLER & MOLZ, 1917
1916	Germany	Halle/Saale	wheat, squareheads	losses 10 %	MÜLLER & MOLZ, 1917
1916	Germany	Coburg	wheat, squareheads	losses up to 50 %	MÜLLER & MOLZ, 1917
	Germany	Württemberg	wheat	severe	LANG, 1918
1921	France	Bassin de Paris	wheat	general	FOËX, 1924
	France	Clermont-Ferrand	wheat	early attack	FOËX, 1924
1923	France	Paris, Centre	wheat	early, losses	FOËX, a.o., 1924
	France	Auvergne	wheat, Bon Fermier	severe, on heads	BEAUVÉRIE, 1923
	Denmark	–	wheat, Panserhvede	new race	BUCHWALD, 1951
	Sweden	–	wheat, Panserhvede	new race	BUCHWALD, 1951
1926	Germany	–	–	severe	STRAIB, 1937 GASSNER & STRAIB, 1933
1927	Germany	–	–	–	GASSNER & STRAIB, 1933
1928	Netherlands	–	wheat, Wilhelmina	also infection on heads	ALABOUVETTE, FEEKES
1929	Denmark	–	spring barley	economically important	BUCHWALD, 1951
1930	Denmark	–	spring barley	localized	BUCHWALD, 1951
	Germany	Hadmersleben	Heines Kolben, a.o.	severe local infection, new race	GASSNER & STRAIB, 1930b
1931	France	Toulousain	–	important	ALABOUVETTE
1935	Germany	Wolfenbüttel	Carstens V	localized	STRAIB, 1939a
1936	France	départements du nord	Joncquois	very severe	HERZOG
	Germany	Braunschweig	barley, Granat gerste	localized	STRAIB, 1939a

[1]) E. & H. = ERIKSSON & HENNING, 1896

Year	Country	Region	Crop	Remarks	Author
1937	Netherlands	Zeeland	Joncquois	severe	VAN DER ZAAG, 1956
	Netherlands	Zeeland	Benoist 40	severe	DROOGENDIJK, 1937
1938	Netherlands	Zeeland, Groningen	Joncquois	severe	VAN DER ZAAG, 1956
1943	England	Southern England	Desprez 80 = Joncquois	rather severe	BROOKS, 1944
	Scotland	Tweed Valley	–	local losses	DENNIS, 1944
1946	England	–	–	quite severe but not exceptional	BATTS & ELLIOTT, 1952
1948	France	Versailles	various varieties	Cappelle race	SIMON & CROISIER, 1959
	Germany	Rheinland, Hessen	Heines IV	new race?	FEEKES, LEIN
1949	Belgium	Gembloux	Blédor	foci	NOULARD
	England	–	Jubilegem = Jubilé	much infected	BATTS & ELLIOTT, 1952
	Netherlands	Noordoostpolder	Heines IV	local infections	FEEKES
1950	Belgium	Gembloux	Blédor	up to 50% losses	NOULARD
	England	–	Jubilegem = Jubilé	much infected	BATTS & ELLIOTT, 1952
1951	England	–	Nord	heavily infected	BATTS & ELLIOTT, 1952
1952	England	Eastern England	Cappelle, Eclipse, Nord	very important, race C2	BATTS, 1957a, b
	Netherlands	–	Cappelle	local infections	FEEKES
	Switzerland	general	Probus	heavy infections	KOBEL, 1955
1953	England	Northern England	–	locally important	BATTS, 1957a, b
	Norway	–	Sigyn II	–	BJAANES, STRAND
1954	England	Kent, Somerset	–	–	BATTS, 1957a, b
	France	Versailles	various varieties	Cappelle race	SIMON & CROISIER, 1959
	Netherlands	Zeeland	Heines VII	new race? locally severe	unpublished reports N.G.C.; BROEKHUIZEN, 1955
	Scotland	Perthshire, Lothians	Eclipse, Nord, Cappelle	locally severe with important losses	BELL; BATTS, 1957a, b
1955	Denmark	-	Nord	severe	ANONYMUS, 1955
	France	Bassin de Paris	various varieties	Cappelle race	SIMON & CROISIER, 1959; unpublished reports N.G.C.
	Netherlands	coastal districts	Heines VII	severe, losses	unpublished reports N.G.C.; BROEKHUIZEN, 1955
	Scotland	Lothians	Cappelle	on heads, losses	BELL
	Switzerland	Northern districts	Probus	severe, losses	KOBEL, 1955
1956	Netherlands	coastal districts	Heines VII	localized	this publication
1957	Belgium	Flanders	Alba, Heines VII	severe, losses	this publication
	Netherlands	general	Alba, Heines VII	very severe, great losses	this publication
	Portugal	general	–	local damage	SANTIAGO
	Switzerland	general	Probus	moderate to severe	this publication
1958	Morocco	oases	–	locally severe	GRANDJOUAN
1959	Netherlands	localized	Triumph	new race	this publication
	Portugal	–	–	rather important	SANTIAGO
1960	Netherlands	localized	Triumph	locally severe	this publication
	Portugal	general	–	important	SANTIAGO

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MAPS

Map 11.3.a The wheat culture in Europe, North Africa and the Near East, and the International Yellow Rust Trials in the Mediterranean area. For the localities of the trials see table A.11.3.
Map from VAN ROYEN: Atlas of the World's Resources, national frontiers changed to the situation in 1960. Each dot represents 5,000 acres (= c. 2,000 ha.) of wheat (winter wheat and spring wheat).

Map 11.3.b The wheat culture and the International Yellow Rust Trials in North-west Europe. For the localities of the trials see table A.11.3.
Map from VAN ROYEN: Atlas of the World's Resources, national frontiers changed to the situation in 1960. Each dot represents 5,000 acres (= c. 2,000 ha.) of wheat (winter wheat and spring wheat).

Map 11.3.c The wheat culture and the International Yellow Rust Trials in the Netherlands. For the localities of the trials see table A.11.3.
Map from: *Landbouwatlas van Nederland* (Oostelijk Flevoland added). Winter wheat: each dot represents 10 ha. (= c. 25 acres); winter wheat and spring wheat: each dot represents c. 16 ha. (= c. 40 acres).

Map 12.22 West-Europe; the wheat-free period in decades. The wheat-free period is the period from harvest time of the spring wheat until sowing time of the winter wheat. The data are derived from the observation forms of the International Yellow Rust Trials Project and from an inquiry of the Netherlands Grain-Centre; the available data are averaged per geographical unit of 1^0 latitude by 1^0 longitude.

Map 36.3 Long distance spore dispersal; European and American data. A map of North America is projected over the map of Europe; both maps are drawn in the same scale. Spore dispersal distances are indicated with arrows; solid arrow – American data; broken arrows – European data. For details see text.

Map 36.4 Approximate areas of cultivation of some interesting varieties. The variety areas include all regions where a variety has been grown regularly for some time; within the boundary lines, however, there may be large regions where the variety is not regularly grown; outside the area the variety may have been grown occasionally.
Widespread varieties are Cappelle, Nord (not in Switzerland) and Heines VII. Local varieties are Hybrid 46, Probus and Staring. Alba, grown in two countries, has the character of a local variety. Epidemics occurred on Alba, Cappelle, Heines VII, Nord, Probus and Staring, Cappelle and Staring being only moderately attacked (24.4,5).

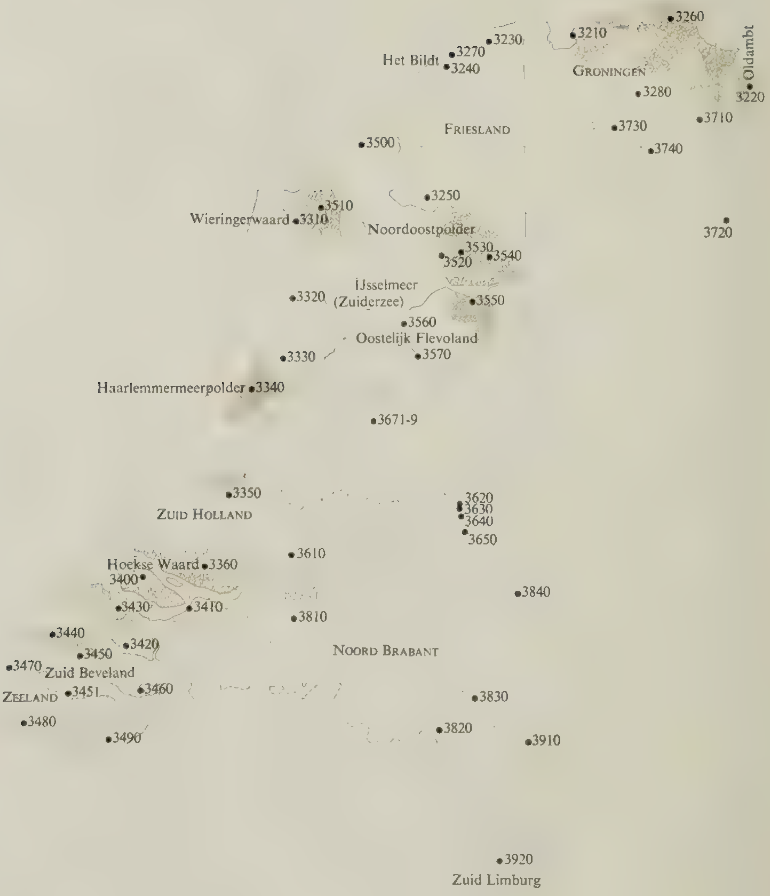
Map 45 North-west Europe, rust pressure map for 1957. The "rust pressure value" is the time in decades between the PA = 50% date of a highly and universally susceptible variety (usually Harvest Queen) and the harvest date. The available rust pressure values are averaged per geographical unit of 1^0 latitude bij 1^0 longitude.

Ireland
6310
Denmark
1610
Poland
2910
Austria
9120
9150
9160
9170
9180
9310
9320
9330
9350
9360
9220
9250
Yugoslavia
Italy
9370
9380
9510
9520
Spain
Portugal
9730
9750
Greece
9610
9620
9630
Turkey
9410
9420
Israel
9910
9920
Egypt
9011

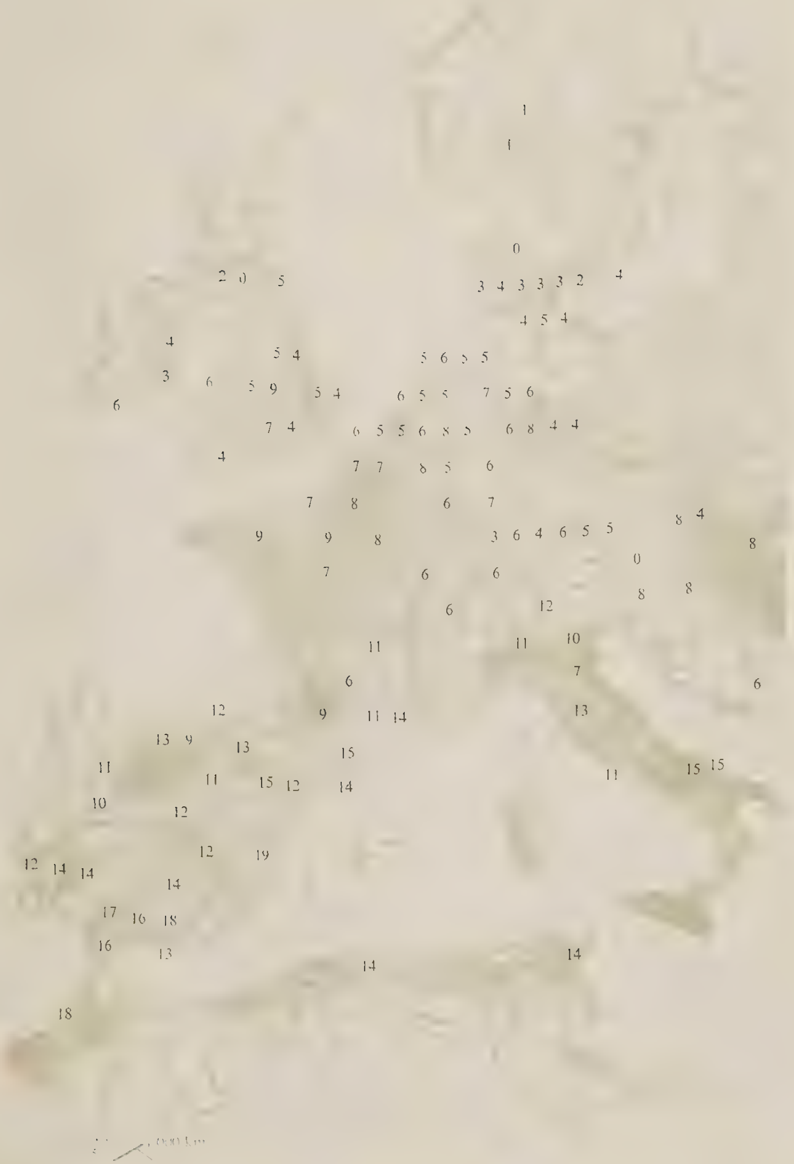
Map 11.3.a

0120
0110
0130
0140
Norway
Sweden
1110
1120
North Sea
Denmark
5110
5120
1130
1410
0420
0410
1310
1420
1210
Great Britain
5310
1230
1220
1510
5910
5210
2120
2110
2810
Ireland
5320
6110
5450
2230
5220
2220
Germany
2210
2240
6210
5510
5440
5430
5610
5520
5620
5410
Netherlands
2250-4
2270
2260
5710
5420
2280
2850
2320
2290
2821
2822
2830
5530
5810
4230
4210
4150
4110
4220
5820
4120
5720
5830
4130
4160
4310
2310
2840
2410
7010
7020
4320
Belgium
2720
Luxemburg
4910
2710
4920
2510
7110
7210
7160
2730
7130
7120
7150
2750
7140
2740
7220
2610
2760
2620
2630
7410
7310
8310
7420
8410
Switzerland
8210
7610
8530
8540
8120
France
8110
8130
Alps
Atlantic Ocean
9310
9320
7320
7720
Italy
9330
7620
Bay of Biscay
9350
9360
7910
7710
Mediterranean
Pyrenees

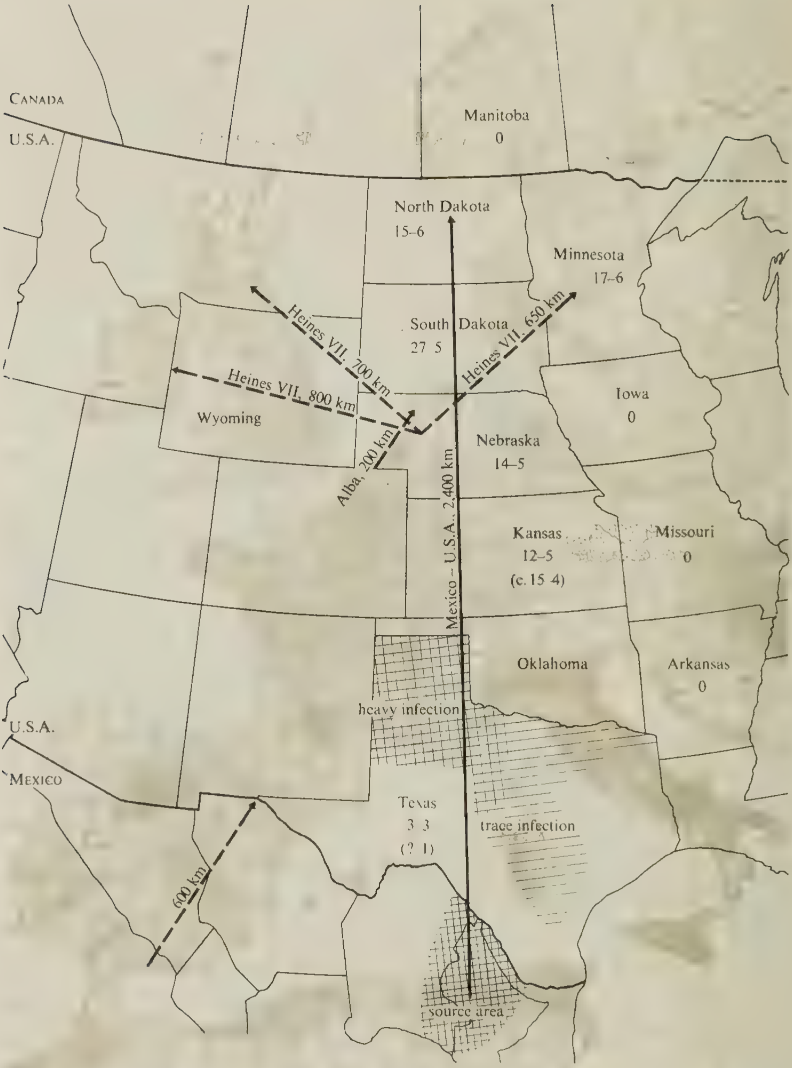
Map 11.3.b


3260
3230
3210
Oldambt
3270
Het Bildt
3240
GRONINGEN
3280
3220
3710
FRIESLAND
3730
3500
3740
3250
3510
Wieringerwaard
3310
Noordoostpolder
3720
3530
3520
3540
IJsselmeer
(Zuiderzee)
3320
3550
3560
Oostelijk Flevoland
3330
3570
Haarlemmermeerpolder
3340
3671-9
3350
3620
3630
3640
ZUID HOLLAND
3650
3610
Hoekse Waard
3360
3400
3840
3430
3410
3810
3440
3420
3450
NOORD BRABANT
3470
Zuid Beveland
ZEELAND
3451
3460
3830
3480
3820
3490
3910
3920
Zuid Limburg

Map 11.3.c



Map 12.22


CANADA
U.S.A.
Manitoba
0
North Dakota
15–6
Minnesota
17–6
South Dakota
27 5
Heines VII, 700 km
Heines VII, 650 km
Heines VII, 800 km
Wyoming
Iowa
0
Alba, 200 km
Nebraska
14–5
Mexico – U.S.A., 2,400 km
Kansas
12–5
(c. 15 4)
Missouri
0
Oklahoma
Arkansas
0
heavy infection
U.S.A.
MEXICO
Texas
3 3
(? 1)
trace infection
600 km
source area

Map 36.3

Cappelle Nord
Heines VII
Hybrid 46
Staring
Alba
Alba
Heines VII
Probus
Cappelle Nord
500 km

Map 36.4

Map 45